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A NEW NEMATODE OF THE GENUS CUCULLANUS (CAMALLANATA : CUCULLANIDAE) FROM A FLOUNDER, PAROPHRYS VETULUS GIRARD, 1854, WITH NOTES ON THE SPECIES FROM PLEURONECTIFORMES[1]

L. MARGOLIS

Abstract

Cucullanus annulatus n. sp., parasitic in the intestine of the pleuronectiform fish *Parophrys vetulus* Girard from coastal waters of British Columbia, is described. The species of *Cucullanus* known from Pleuronectiformes are reviewed. *Cucullanus wülkeri* Kreis is considered a synonym of *C. heterochrous* (Rudolphi).

The lemon sole or English sole, *Parophrys vetulus* Girard, 1854, a member of the family Pleuronectidae of the order Pleuronectiformes (= Heterosomata), is found along the Pacific coast of North America, from southern California to northwestern Alaska. In the coastal waters of British Columbia this fish harbors a species of *Cucullanus* which does not appear to have been reported previously. The name *Cucullanus annulatus* n. sp. is proposed for it.

The material examined consists of the following: 14 males collected from one host from Baynes Sound, east coast of Vancouver Island, on October 12, 1951; 5 males, and 11 males and 8 females, collected from two hosts, respectively, from near Dodd's Narrows, east coast of Vancouver Island, on December 30, 1952; 5 males and 8 females collected from one host from Union Bay, east coast of Vancouver Island on May 25, 1954; 14 males and 5 females, and 9 males and 7 females, collected from two hosts, respectively, from near Dodd's Narrows on March 28, 1958; and 26 males and 15 females collected from one host from near Dodd's Narrows on May 4, 1959.

Measurements in the following description are based on 41 males and 19 mature (egg-bearing) females. Unless otherwise stated, measurements in the description of the female refer only to the mature specimens. No attempt was made to separate the males on the basis of maturity or immaturity.

Description of *Cucullanus annulatus* n. sp.

(Figs. 1–13)

Males are small, slender nematodes, 2.21 to 5.50 mm in length, with the anterior end bent dorsad to a varying degree and the tail curved strongly ventrad. The slightly swollen head measures 0.12 to 0.18 mm in diameter.

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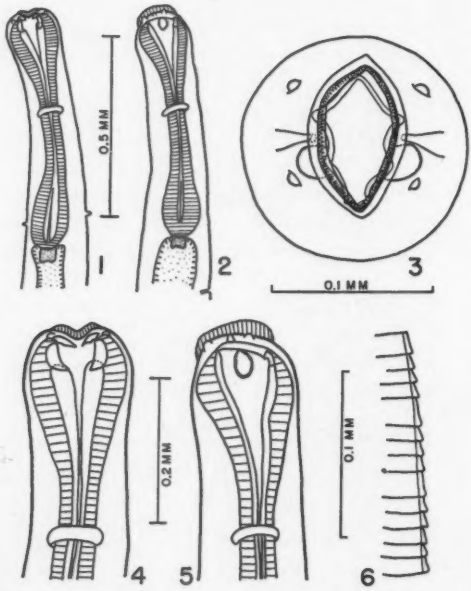
Behind the head the body narrows towards the midoesophageal region, then enlarges again to a width of 0.10 to 0.25 mm just behind the oesophagus. In specimens longer than about 3.5 mm the maximum body diameter is attained at this level. In specimens up to about 3.5 mm in length, this postoesophageal body diameter is usually slightly less than the diameter at the head end. The body tapers more or less gradually from the postoesophageal region to the cloacal opening and then abruptly to the pointed posterior extremity. The tail is 0.083 to 0.13 mm in length.

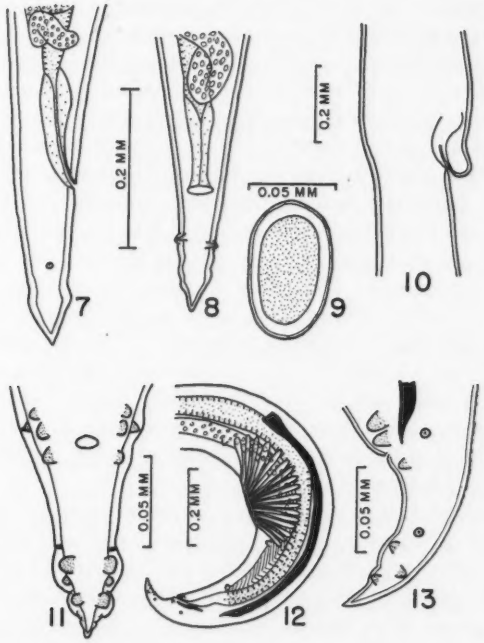
The cuticle is 0.002 to 0.005 mm thick. It appears to be devoid of transverse striations in the posterior half of the body. At about mid-length of the body, very fine cuticular striations are barely discernible. Proceeding anteriorly the striations gradually become more definite and farther apart. They are more distinct ventrally than dorsally. Ventrally, from a short distance posterior to the oesophageal–intestinal junction to the anterior oesophageal swelling, the striations are so prominent as to be more properly termed annulations. These annulations become less marked laterally and are completely absent dorsally. When viewed laterally the cuticle of the anteroventral region has a serrated appearance as a result of the prominent annulations. The distance between the annulations gradually decreases anteriorly and is 0.0042 to 0.0097 mm.



FIGS. 1–6. *Cucullanus annulatus* n. sp. All figures drawn with the aid of a camera lucida.
FIGS. 1 and 4. Anterior end of male, ventral view.
FIGS. 2 and 5. Anterior end of male, lateral view.
FIG. 3. Anterior end of male, *en face* view.
FIG. 6. Cuticle of the ventral oesophageal region of female, lateral view.

The mouth is dorsoventrally elongated. Attached to the cuticular collar surrounding the mouth is a continuous membranous flange bearing many small teeth on its internal face. There are four submedian cephalic papillae and a pair of lateral amphids arranged as shown in Fig. 3. Internally there is a chitinous framework around the mouth opening. A pair of bean-shaped chitinous structures project posteriorly from a ventrolateral margin of the circumoral chitinous framework. In lateral view these structures are roughly oval-shaped and in ventral view they show a concave inner margin and a convex outer margin.

The oesophagus, 0.43 to 0.70 mm in length, is enlarged anteriorly, narrows towards its mid-length, and expands again to a club-shaped swelling posteriorly. The anterior swelling, 0.10 to 0.16 mm in diameter, is always more pronounced than the posterior one, which measures 0.065 to 0.11 mm in diameter. At its mid-length the oesophagus has a diameter of 0.038 to 0.057 mm. The ratio of oesophagus length to body length decreases from about 1:5 in the smallest specimen to about 1:8 in the largest specimen. The oesophagus



FIGS. 7–13. *Cucullanus annulatus* n. sp. All figures drawn with the aid of a camera lucida.
FIG. 7. Posterior end of female, lateral view.
FIG. 8. Posterior end of female, ventral view.
FIG. 9. Unsegmented ovum.
FIG. 10. Vulvar region, lateral view.
FIG. 11. Posterior end of male, ventral view.
FIGS. 12 and 13. Posterior end of male, lateral view.

is lined with chitin except for a short distance at the posterior end. A two-lobed valve projects from the oesophagus into the intestine. The intestine opens into a short rectum, which also receives the ejaculatory duct to form a cloaca. The cloacal opening may or may not be set on a prominent elevation, presumably depending on the state of contraction of the muscles in the caudal region.

The nerve ring is 0.21 to 0.30 mm from the anterior extremity. The lateral cervical papillae are situated 0.026 to 0.097 mm in front of the junction of the oesophagus and intestine or 0.37 to 0.59 mm from the anterior end. The left cervical papilla is often a little more anterior than the right one.

The excretory pore lies 0.057 to 0.17 mm behind the oesophagus.

The testis originates at about the level of or slightly anterior to the anterior margin of the preanal sucker. It follows a straight course anteriorly, reaching to within 0.08 to 0.60 mm of the oesophagus before turning on itself and proceeding backwards to join the seminal vesicle.

The preanal sucker, in lateral view, appears as a fan-shaped group of muscles which, when contracted, takes on the form of a cup-shaped sucker. In ventral view this sucker is oval-shaped. Its length is 0.14 to 0.29 mm and its posterior margin is 0.18 to 0.37 mm in front of the anus.

There are 11 pairs of caudal papillae. The two anterior pairs are the largest, one pair lying immediately anterior to the preanal sucker and the second pair lying just posterior to or on the posterior margin of the sucker. The third pair lies at about 2/5 to 3/5 the distance from the sucker to the anus. These three pairs of preanal papillae are subventral. The fourth and fifth pairs are also subventral, lying one behind the other immediately in front of and lateral to the anus. The sixth pair is lateral and is at about the same level as the fifth pair. The seventh pair, subventral, lies immediately behind the anus or at its posterior margin. The remaining four pairs of papillae lie some distance behind the adanal group. The eighth pair is lateral and is the smallest of all the caudal papillae. The most posterior or 11th pair is subventral. Of the two pairs of papillae between the 8th and 11th pairs, one pair is lateral or subdorsal and the other pair is subventral. The relative position of these two pairs is somewhat variable. Usually the subventral papillae lie in front of or at about the same level as the lateral or subdorsal ones but occasionally they are situated behind the lateral or subdorsal pair.

The slender spicules, 0.47 to 0.76 mm in length, are pointed distally and slightly enlarged proximally. When completely retracted they extend to almost the middle of the preanal sucker or beyond. The accessory piece measures 0.065 to 0.085 mm in length by 0.0081 to 0.0097 mm in breadth.

Females are larger than the males. Mature (egg-bearing) specimens are 5.16 to 9.43 mm in length. Of two specimens of length 5.16 mm, eggs were present in the uterus of one but not in the other. The dorsal flexure of the head usually is not as pronounced as in the male. The body diameters at the head and at the posterior end of the oesophagus are 0.12 to 0.15 mm and 0.15 to 0.21 mm, respectively. The maximum body width, 0.17 to 0.27 mm, is

attained at about 1/6 the length from the anterior end. The posterior end tapers sharply from a short distance anterior to the anus to the pointed tip of the tail, which is 0.15 to 0.24 mm in length.

Nineteen immature females, excluding the specimen of length 5.16 mm, measured 1.94 to 4.68 mm in length. In immature specimens of length greater than 3 mm the body diameter increases to a maximum at the level of the junction of the oesophagus and the intestine and then decreases uniformly to the tail. In specimens less than about 3 mm in length the body tapers gradually from the head to the tail.

The cuticle is 0.004 to 0.008 mm thick. Faint cuticular striations were seen in the posterior half of the body of some and may be present in all specimens. At about mid-length of the body, fine striations are apparent in all specimens and proceeding anteriorly they become more distinct and farther apart. Approaching the junction of the anterior and middle thirds of the body the striations gradually transform into marked annulations which can be seen both dorsally and ventrally. Ventrally these annulations extend to the region of the anterior oesophageal swelling and dorsally they are present to the mid-length of the oesophagus. The distance between the annulations decreases anteriorly and is 0.0065 to 0.023 mm. In immature females the annulations are most prominent ventrally in the oesophageal region, similar to the condition observed in males.

The mouth and associated structures are as in the male.

The oesophagus has the same shape as in the male but the anterior swelling is less pronounced. The diameters at the anterior swelling, at the mid-length, and at the posterior swelling are 0.10 to 0.13 mm, 0.049 to 0.070 mm, and 0.087 to 0.12 mm, respectively. Generally, the diameter of the anterior oesophageal swelling is greater than that of the posterior swelling, the difference between these diameters decreasing with increased body length. In a specimen of 9.43 mm in length the posterior swelling is just slightly larger than the anterior one. In immature specimens the difference in diameters of the two oesophageal swellings is more pronounced than in mature specimens and reaches a maximum in the smallest specimen. The length of the oesophagus is 0.64 to 0.92 mm or 1/8 to 2/25 of the length of the body of mature specimens. Generally, the ratio of oesophagus length to body length increases with decreased body length and in an immature female of length 1.94 mm it is 1:4.3.

The nerve ring lies 0.28 to 0.33 mm from the anterior extremity.

The lateral cervical papillae are 0.07 to 0.16 mm anterior to the posterior end of the oesophagus or 0.53 to 0.76 mm from the anterior end of the body. Another pair of lateral papillae occur at about mid-length of the tail or a little farther behind.

The excretory pore is 0.10 to 0.29 mm posterior to the oesophagus.

The vulva, overhung by a very prominent anterior lip, is situated 3.1 to 6.1 mm (55.5% to 66.7% of total body length) from the anterior end. The vagina is directed anteriorly and joins the two divergent uteri, which, in fully mature individuals, contain many eggs. The eggs have a thin shell and measure 72 to

85 μ in length by 42 to 50 μ in width. The posterior ovary is 0.073 to 0.17 mm from the anus and the anterior ovary is 0.11 to 0.66 mm from the posterior end of the oesophagus.

Type host: Parophrys vetulus Girard (family Pleuronectidae).

Type locality: Dodd's Narrows, east coast of Vancouver Island, British Columbia.

Type specimens: Holotype male, allotype female, and paratypes to be deposited in the National Museum, Ottawa, Canada.

Discussion

The genus *Cucullanus* is a large one, more than 70 species having been described. Campana-Rouget (2), in a revision of the subfamily Cucullaninae, reported 65 species (plus 2 varieties), 16 of which are cited as *sp. inquirenda*. At least six more species are known, these having been described by Karve (8), Yamaguti (19), and Khera (9). The principal hosts are fishes. Only four species are known from other hosts, namely chelonians.

Cucullanus annulatus appears to be unique among this large group of species because the fine transverse cuticular striations become more marked anteriorly, giving rise to prominent annulations. These annulations impart to the margins of the cuticle a serrated appearance. Other species apparently do not show this transition from fine cuticular striations to annulations in the anterior region of the body. In three species from chelonians, namely *C. serratus* (Lane, 1916), *C. niloticus* Campana-Rouget, 1957, and *C. hardellus* Khera, 1956, prominent cuticular annulations (or serrations) are present in addition to the fine striations for almost the entire length of the body; the annulations do not replace the striations as in *C. annulatus*. These species from chelonians differ from *C. annulatus* in many other morphological characters, including the arrangement of the postanal papillae, absence of a very prominent anterior vulvar lip, position of the excretory pore, body and spicule lengths, and various other measurements.

Dacnitis squali Dujardin, 1845, from *Galeus galeus*, possesses a cuticle which seems to be most similar to that of *C. annulatus*. Dujardin (6) described the cuticle as follows: "tégument à stries transverses de Omm, 014, et paraissant denté en scie sur les bords". The brief description of one female does not permit a decision, on morphological grounds, as to whether the species is truly a *Dacnitis* or whether it should be transferred to *Cucullanus*. Even if it proves to be a species of *Cucullanus*, its large size (length of the female, 18.5 mm) would seem to exclude the possibility that it is identical with *C. annulatus*.

Up to the present time only one species, *Cucullanus smedleyi* Campana-Rouget, 1957 (= *C. elongatus* Smedley, 1933), has been recorded from marine fishes from the Pacific coast of North America. It was described by Smedley (14) from *Ophiodon elongatus* taken in British Columbia waters. *Cucullanus smedleyi* is a much larger species than *C. annulatus*; the males measure up to 30 mm in length and the females up to 40 mm in length. In addition to the extreme difference in size, with accompanying differences in measurements of

various structures, four features are noticeably different in the two species. (1) The cuticle of *C. smedleyi* lacks the annulations noted in the anterior region of *C. annulatus*. (2) The anterior region of *C. smedleyi* is not curved dorsally as is that of *C. annulatus*. (3) The oesophagus of *C. smedleyi* is divided into two regions, a coarsely muscular anterior portion (about 1/4 to 1/3 of the total oesophagus length) and a more finely muscular posterior portion. A similar distinction of two oesophageal regions is not apparent in *C. annulatus*. (4) The testis of *C. smedleyi* is much convoluted, whereas that in *C. annulatus* follows a straight course anteriorly and then posteriorly.

While differing considerably from *C. smedleyi*, *C. annulatus* shows strong similarities to several species of *Cucullanus*, particularly *C. heterochrous*, recorded from Pleuronectiformes from distant geographical regions.

Campana-Rouget (2) listed seven species of *Cucullanus*, one of which was not named, from Pleuronectiformes. These are *C. heterochrous* Rudolphi, 1802; *C. minutus* Rudolphi, 1819; *C. antipodeus* Baylis, 1932; *C. cylindricus* (Chandler, 1935) Campana-Rouget, 1957; *C. pleuronectidis* (Yamaguti, 1935) Campana-Rouget, 1957; *C. gendrei* Campana-Rouget, 1957; and *Cucullanus* sp. Campana-Rouget and Chabaud, 1956.

On the basis of available descriptions and illustrations, *Cucullanus annulatus* appears to differ consistently from these species not only in the possession of transverse cuticular annulations in the anterior region of the body but also in the possession of a very prominent anterior vulvar lip.

Notes on the Species of *Cucullanus* from Pleuronectiformes and Comparisons with *C. annulatus*

1. *Cucullanus heterochrous* is a well-known parasite of several species of Pleuronectidae and Soleidae from European waters and it has also been reported from the coast of French West Africa.

The measurements generally quoted for this species suggest that it is larger than *C. annulatus*. Törnquist (15), in a very detailed redescription of *C. heterochrous*, gave the following range of measurements for 10 specimens of each sex: males, 7.067 to 8.938 mm in length by 0.219 to 0.289 mm in maximum width; females, 8.674 to 11.186 mm in length by 0.281 to 0.406 mm in maximum width. In a footnote on page 74 he stated that he had not included in this range of measurements a male 9.158 mm and a female 12.543 mm in length. Also, in context, Törnquist gave spicule and other measurements of a male, 6.5 mm in length. The lengths of several apparently immature specimens were given by Törnquist as follows: the smallest individual was 1.763 mm in length; a female in which the vulva was poorly differentiated was 1.81 mm in length; a male in which the preanal sucker was weakly developed was 3.214 mm in length; and a male in which the preanal sucker was well marked was 4.321 mm in length. Törnquist's data were only partially utilized in recent publications by Dollfus (5) and Campana-Rouget (2), who cited the lengths of males and females as 7 to 9 mm and 8.6 to 12.5 mm, and 7 to 8.9 mm and 8.6 to 11.18 mm, respectively. In a paper preceding that of Törnquist, Gendre (7) recorded

the measurements of a male and female as 9.03 mm in length by 0.35 mm in width and 10.74 mm in length by 0.35 mm in width, respectively. More recently Kreis (10) reported the measurements of a male as 8.26 mm in length by 0.405 mm in maximum width, and those of females as 8.69 to 12.03 mm in length by 0.426 to 0.495 mm in width.

Smaller specimens, apparently mature, than those reported by the preceding authors have been described. Wülker (16) examined a large amount of material from *Pleuronectes flesus* and *P. platessa* from the North Sea and gave the size of males as 4.4 to 6.84 mm (mean 5.1 mm) in length by 0.20 to 0.23 mm (mean 0.23 mm) in width, and that of females as 6.3 to 10.4 mm (mean 8.0 mm) in length by 0.25 to 0.39 mm (mean 0.34 mm) in width. Punt (13) recorded measurements of one male and five females from *Pleuronectes* spp. from the North Sea as 5.9 mm in length by 0.2 mm in width, and 6.9 to 8.5 mm in length by 0.16 to 0.25 mm in width, respectively.

The measurements given by Wülker and Punt, both of whom recorded their specimens as *C. platessae* Rudolphi, 1809 (an accepted synonym of *C. heterochrous*), actually indicate that the size range of *C. heterochrous* overlaps with that of *C. annulatus*. Nevertheless, the measurements of body size given by various authors demonstrate that the maximum length of *C. heterochrous* is in excess of the known maximum length of *C. annulatus*.

Little difference exists between measurements of structures or organs of *C. heterochrous* and *C. annulatus* and such differences as do exist are approximately in proportion to the larger body size of *C. heterochrous*. Punt's measurement of 4.8 mm for the length of the spicules in a male of length 5.9 mm is probably a misprint for 0.8 or 0.84 mm.

Kreis (10) named *Cucullanus wülkeri* for Wülker's (16) specimens of *C. platessae* on the basis of the existence of only six pairs of caudal papillae in the male (three preanal and three postanal pairs) as described by Wülker. This small number of papillae in a species of *Cucullanus* is not in accord with the generic concept. The males of all species of *Cucullanus* are considered to be supplied with 11 pairs of caudal papillae. Wülker apparently overlooked the four pairs of adanal papillae and the smallest pair of postanal papillae. Törnquist (15, footnote, page 65) has already pointed out that Wülker's description of the caudal papillae was incorrect. It appears that *C. wülkeri* is another synonym of *C. heterochrous*.

2. *Cucullanus minutus* is another species common to some Pleuronectidae in Europe and has also received detailed morphological treatment by Törnquist (15). It is a shorter but considerably stouter worm than *C. annulatus* and possesses an intestinal caecum. According to Törnquist, males measure 2.62 to 3.39 mm in length by 0.27 to 0.39 mm in maximum width and females measure 2.53 to 3.49 mm in length by 0.34 to 0.53 mm in maximum width. Wülker (16) gave the size of the male and female as 3.7 mm by 0.39 mm and 5 mm by 0.56 mm, respectively. There are four pairs of subventral adanal papillae in males of *C. minutus* in contrast with three pairs of subventral and one pair of lateral adanal papillae in the males of *C. annulatus*, as well as in other *Cucullanus* spp. from Pleuronectiformes.

3. *Cucullanus antipodeus* was described by Baylis (1) from *Rhombosolea* sp. (family Pleuronectidae) from New Zealand. It is a larger species (males 6 to 8.7 mm in length and females 8.7 to 19.6 mm in length) than *C. annulatus*, but the spicules (0.45 to 0.5 mm in length) and gubernaculum (0.045 mm in length) are shorter. The cervical papillae, located a little behind the nerve ring, are farther forward than in *C. annulatus*, in which they are closer to the posterior end of the oesophagus than to the nerve ring. In *C. antipodeus* the eighth pair of caudal papillae in the male is lateral to the ninth pair and located at their base, whereas in *C. annulatus* the eighth pair of caudal papillae is lateral but distinctly anterior to the ninth pair. A unique feature of *C. antipodeus* is that the eggs contain coiled embryos at the time of deposition.

Khera (9) recorded a species as *C. antipodeus* from a non-pleuronectiform fish from Lucknow, India. He noted that his specimens differed from those of the original author of the species in the greater number of caudal papillae (14 pairs as compared to 11 pairs) and in a longer gubernaculum (0.077 mm as compared to 0.045 mm). The increased number of caudal papillae is due to a greater number of postanal rather than preanal papillae. Also, his illustration of the anterior end of a female shows the cervical papillae lying close to the posterior end of the oesophagus, whereas Baylis (1) described them as lying a little behind the nerve ring. In view of these differences, particularly in the number of caudal papillae, it is not unlikely that Khera was dealing with a species distinct from *C. antipodeus*. In fact the number of postanal papillae observed by Khera is unique among the Cucullanidae. In members of the genus *Neocucullanus* sensu Campana-Rouget, 1957 (2) there are more pairs of preanal papillae than in *Cucullanus*, but the number of adanal and postanal papillae is the same.

4. *Cucullanus cylindricus* was named by Chandler (4), as *Dychelyne cylindricus*, for *Ascaris* (?) sp. Linton, 1901 from *Paralichthys dentatus* (family Bothidae) from the Atlantic coast of the United States. This species is known only from females and is very poorly characterized. Nevertheless, from Linton's (11) brief description and illustrations, it is apparent that the species differs from *C. annulatus*. Linton stated that the diameter is about 1/10th of the body length, thereby being a much stouter worm than *C. annulatus*, and a long dorsal intestinal caecum as well as a short ventral intestinal caecum are present. *Cucullanus annulatus* lacks an intestinal caecum. Linton gave the body measurements of an apparently gravid female as 4 mm in length and 0.38 mm in maximum diameter, indicating that the species is not only stouter, but is also shorter than *C. annulatus*.

In a later paper, Linton (12) assigned *Ascaris* (?) sp. to *Heterakis* sp. and recorded a female specimen, which he stated "is similar to *Ascaris* (?) sp.", from *Lophopsetta maculata* (family Bothidae), and several females, which he stated "appear to be identical with *Ascaris* (?) sp.", from *Paralichthys albiguttus*. Campana-Rouget (2) considered these specimens to be cospecific with *C. cylindricus*. Accurate specific determination of Linton's material will require a re-examination of his specimens or a study of new collections from the same hosts and localities.

5. *Cucullanus pleuronectidis* was described by Yamaguti (17, 18), from various flatfishes of the families Pleuronectidae and Bothidae from Japan. Males measured 3.15 to 8 mm in length by 0.175 to 0.35 mm in width, and ovigerous females measured 5.5 to 11 mm in length by 0.3 to 0.65 mm in width. This species thus attains a greater length than that known for *C. annulatus* and is relatively somewhat stouter. The length of the gubernaculum, 0.033 to 0.04 mm, is about 1/2 of that in *C. annulatus* and the preanal sucker, 0.51 to 0.65 mm in front of the anus, is more anteriorly located than that in *C. annulatus*, in which the corresponding measurement is 0.18 to 0.37 mm. A ventral intestinal caecum, absent in *C. annulatus*, is present in *C. pleuronectidis*. The vagina in *C. pleuronectidis* is directed posteriorly rather than anteriorly as in *C. annulatus*. According to the illustration of *C. pleuronectidis* in Yamaguti's (17) earlier paper, the posterior oesophageal swelling is much more pronounced than the anterior one, but the measurements given in the later paper (Yamaguti (18)) suggest that in the smaller specimens the anterior swelling may be more marked. In *C. annulatus* the anterior oesophageal swelling is greater than the posterior one except in the largest female.

6. *Cucullanus gendrei* was described by Campana-Rouget (2) from *Syacium micrurum* (family Bothidae) from the coast of French West Africa. This species again is stouter than *C. annulatus* but the females are shorter. Measurements recorded for the males and females are, respectively, 3.03 to 4 mm in length by 0.31 mm in width and 3.2 to 6 mm in length by 0.38 mm in width. However, it was not stated whether all females in this length range were egg-bearing. Other differences in measurements between *C. gendrei* and *C. annulatus* are the longer tail, longer gubernaculum, longer oesophagus, greater distance of the nerve ring from the anterior end of the body, and the smaller eggs in the former species. The excretory pore lies anterior to the end of the oesophagus in *C. gendrei* but posterior thereto in *C. annulatus*. The posterior oesophageal swelling is more pronounced than the anterior one in *C. gendrei*, whereas the reverse prevails in *C. annulatus*, and a prominent postanal lip is present in *C. gendrei* but not in *C. annulatus*.

7. *Cucullanus* sp. Campana-Rouget and Chabaud, 1956 (3) is known only from three females taken from *Solea solea* from near Banyuls on the Mediterranean coast of France. Although they are about the same length as *C. annulatus* they are apparently a little stouter. A specimen of *Cucullanus* sp. of 8.23 mm in length had a maximum width of 0.35 mm, whereas females of *C. annulatus* up to 9.43 mm in length have a maximum width of 0.27 mm. The tail (0.27 mm) is a little longer and the eggs (0.061 to 0.067 mm by 0.038 mm) smaller in *Cucullanus* sp. The cervical papillae are at the level of the posterior extremity of the oesophagus in *Cucullanus* sp., whereas in *C. annulatus* they are located anterior to this region.

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ARTIFICIAL KEY TO THE MYSIDACEA OF THE CANADIAN ATLANTIC CONTINENTAL SHELF[1,2]

PIERRE BRUNEL[3]

Abstract

A key is given for the identification of 16 species and one variety of Mysidacea recorded up to date in waters of the Canadian Atlantic continental shelf. Two species not yet recorded but likely to occur in these waters are also included. The key is to be used with Tattersall's Review of the Mysidacea of the U.S. National Museum (1951). Diagnostic characters of four species are illustrated.

The following key has been extracted from the literature to help marine ecologists, fishery biologists, and other naturalists identify rapidly at least the most common species of Mysidacea (Crustacea, Malacostraca) occurring from the tidal zone to the upper part of the continental slope off the Canadian Atlantic coasts. For the fauna of the continental slope and deeper water, the two comprehensive works of Tattersall and Tattersall (8) and W. M. Tattersall (7) should be used together; the former alone has keys.

The species included in the key are those recorded from Canadian Atlantic waters in the basic list of W. M. Tattersall (6), to which have been added the following, recorded since that time:

Boreomysis tridens var. *lobata* n. var.: Nouvel (4)
Mysis gaspensis n. sp.: O.S. Tattersall (5)
Pseudomma affine G. O. Sars: Klawe (3)
Heteromysis formosa S.I. Smith: Bousfield (1)
Mysis litoralis (Banner): Holmquist (2)

Moreover, *Mysis relicta* Lovén and *Mysis polaris* Holmquist are included in the key, although they have not yet been recorded from the area considered, since it is not impossible that they may be found there. The common bathypelagic genera *Gnathophausia* and *Eucopia* are included in the key to genera since some stray individuals could occasionally be taken near the continental edge, but no key to their species is given.

The key is abridged primarily from those given by Tattersall and Tattersall (8) for British Mysidacea, modified to include Canadian species as described or figured by W. M. Tattersall (7) and Holmquist (2). References to diagnostic figures of every species are given in parentheses in the keys after the names of the species. These figures should always be checked after an identification, especially since the two monographs referred to are readily available.

For the sake of making the key swiftly available, no systematic examination even of the collection of Mysidacea of the Station de Biologie marine could be

[1]Manuscript received May 18, 1960.
[2]Contribution No. 76, Département des Pêcheries, Quebec.
[3]Station de Biologie marine, Grand River, Gaspé, Quebec.

undertaken. It can be noted, however, that specimens of the following species from the Gulf of St. Lawrence are available in the latter collection:

Boreomysis tridens	*Stilomysis grandis*
Mysis mixta	*Pseudomma truncatum*
Mysis stenolepis	*Erythrops erythrophthalma*
Mysis gaspensis	*Meterythrops robusta*

Key to the Genera

1. Branchiae present on all or some of the thoracic limbs. Pleopods well developed in both sexes, natatory, unmodified. No statocyst. Marsupium with seven pairs of brood lamellae (oostegites). Bathypelagic 2
   Branchiae absent. Pleopods of female reduced, rudimentary; of male variable. Marsupium usually with less than seven pairs of oostegites. Statocyst usually present 3

2. Pleural plates of abdominal somites distinct and moderately well developed. Telson with distal constriction preceding bifurcate tip ..... *Gnathophausia*
   No pleural plates on abdominal somites. Outer margin of antennal scale naked. Telson entire ..... *Eucopia*

3. Exopod of uropod with proximal portion of outer margin naked, marked distally by one or two spines and an incipient articulation. Telson cleft. Statocyst present. Marsupium with seven pairs of oostegites ..... *Boreomysis*
   Exopod of uropod undivided 4

4. Telson entire or with a small unarmed apical incision 5
   Telson cleft 6

5. Antennal scale setose all around. Telson linguiform, margins armed with many spines in series 7
   Antennal scale with outer margin naked and ending distally in a thorn. Lateral margins of telson with few or no spines 8

6. Telson, lateral row of spines extending from base to, or nearly to, apex ..... *Mysis*
   Telson, lateral row of spines extending only from middle of lateral margin to apex ..... *Heteromysis*

7. Antennal scale very long (about 4 times as long as last two joints of antennal peduncle), slender, acutely pointed. In male, fourth pair of pleopods, exopod two-jointed with a pair of stout apical barbed setae ..... *Neomysis*
   Antennal scale shorter (about 3½ times as long as last two joints of antennal peduncle), broader, apically blunt. In male, fourth pair of pleopods, exopod four-jointed with a pair of stout apical barbed setae and one similar seta at distal end of third joint .... *Stylomysis*

8. Eyes rudimentary, without visual elements, fused to form a median plate (ocular plate) ..... *Pseudomma*
   Eyes well developed with functional visual elements 9

9. Telson shorter than broad, apex very widely truncate and armed with spines. Eyes reniform, pigment bright red (yellow in preservative liquids) ..... *Erythrops*
   Telson longer than broad, tapering, apex very narrowly truncate, armed with spines. Eyes large and globular, pigment black ..... *Meterythrops*

Keys to Species

Boreomysis G. O. Sars 1869

1. Rostral plate produced into three outgrowths, one median (rostrum) and two lateral .. 2
   Rostral plate produced into a single median rostrum 3

2. Rostral plate with lateral outgrowths acute ..... *B. tridens* G. O. Sars 1870 (Tattersall and Tattersall (8), Figs. 19–21)
   Rostral plate with lateral outgrowths rounded, lobe-like ..... *B. tridens* var. *lobata* Nouvel 1942 (Nouvel (4), Fig. 1)

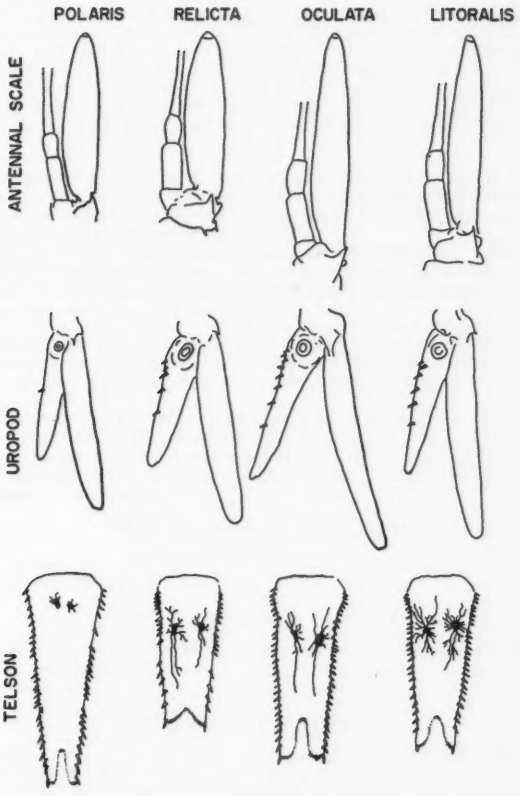

FIG. 1. Some diagnostic characters of *Mysis polaris*, *M. relicta*, *M. oculata*, and *M. litoralis*. Setation is not shown on the antennal scales and uropods. (After Holmquist (2).)

3. Rostral plate produced into a well-developed median, acute spiniform process. Tip of antennal scale transversely truncated.....*B. arctica* (Kröyer) 1861 (Tattersall and Tattersall (8), Figs. 19, 21–22)
Rostral plate produced into two closely appressed acute spiniform processes. Tip of antennal scale obliquely truncated.....*B. nobilis* G.O. Sars 1879 (W. M. Tattersall (7), Fig. 6)

Mysis Latreille 1802

1. Antennal scale short and broad, 4 to 5 times as long as broad, apically blunt..... 2
Antennal scale more elongated, more than 5 times as long as broad, apically blunt or acute..... 3

2. Telson short and broad, about 3½ times as long as broad at the apex; margins nearly parallel, each with less than 20 spines; apical cleft shallow and broadly open. Uropod, inner margin of endopod with three to five spines. Fresh water, not yet found in brackish water in Canada.....*M. relicta* Lovén 1862 (present paper, Fig. 1)
Telson long and narrow, from 8 to 9 times as long as broad at the apex; margins converging, each with more than 25 spines; apical cleft deep and narrow. Uropod, inner margin of endopod with one spine. Not yet recorded, but likely to occur in Arctic Canada.....*M. polaris* Holmquist 1959 (present paper, Fig. 1)

3. Antennal scale from 5 to 6 times as long as broad, apically blunt..... 4
Antennal scale more than 9 times as long as broad, apically acute..... 6

4. Telson short and broad, less than 4 times as long as broad at the apex; lateral margin with a row of 20–22 spines extending from base of telson only to level of base of median cleft; four chromatophores or more. Uropod, inner margin of endopod with four spines ..... *M. gaspensis* O.S. Tattersall 1955 (O.S. Tattersall (5), two figures)
Telson longer and narrower, more than 4 times as long as broad at the apex; margin with a row of 25 or more spines extending distally farther than level of base of median cleft; four chromatophores or less. Uropod, inner margin of endopod with six or more spines 5

5. Telson with 25–30 spines on lateral margin, extending from base to apex, with about four spines distal to base of median cleft; the latter deep and narrow, rounded proximally, its margins subparallel. Uropod, inner margin of endopod with seven to eight spines ..... *M. oculata* (Fabricius) 1780 (present paper, Fig. 1)
Telson with row of about 25 spines on lateral margin, extending from base to a point between apex and level of base of median cleft; the latter broader at the apex, rather acute proximally, subtriangular. Uropod, inner margin of endopod with about six spines ..... *M. litoralis* (Banner 1948) (present paper, Fig. 1)

6. Antennal scale about 9 times as long as broad, outer margin nearly straight. Telson comparatively deeply cleft, spines of lateral margin more than 30, extending almost to the apex, at least 3 or 4 on the margin posterior to base of cleft.... *M. mixta* Lilljeborg 1852 (W. M. Tattersall (7), Fig. 63)
Antennal scale about 12 times as long as broad, outer margin concave. Telson comparatively less deeply cleft, spines on the lateral margin about 25, the most distal spine at about the level of base of cleft, so that there is a considerable unarmed posterior portion of the lateral margin..... *M. stenolepis* S.I. Smith 1873 (W. M. Tattersall (7), Fig. 64)

Heteromysis S. I. Smith 1873

Single species found in the area..... *H. formosa* S. I. Smith 1873 (W. M. Tattersall (7), Fig. 100)

Neomysis Czerniavsky 1882

Single species found in the area (key to the species of the world in W. M. Tattersall (7), p. 180) ..... *N. americana* (S. I. Smith) 1873 (W. M. Tattersall (7), Fig. 77)

Stilomysis Norman 1892

Single species found in the area..... *S. grandis* (Goës) 1863 (W. M. Tattersall (7), Fig. 66)

Pseudomma G. O. Sars 1870

1. Ocular plate, serrations occupying more than half of anterolateral margin. Telson with at least four pairs of apical spines. Antennal scale more than 4 times as long as its greatest width..... *P. affine* G. O. Sars 1870 (Tattersall and Tattersall (8), Fig. 52)
Ocular plate, serrations occupying about a third of anterolateral margin. Telson with two, sometimes three pairs of apical spines. Antennal scale less than 4 times as long as its greatest width 2

2. Ocular plate about 3½ times as broad as long, with its lateral margins almost parallel; edges of its anterior median cleft not in contact with each other, cleft being triangular. Antennal scale less than 3 times as long as its greatest width . *P. truncatum* S. I. Smith 1879 (W. M. Tattersall (7), Fig. 47)
Ocular plate about 2½ times as broad as long, with lateral margins not parallel; its anterior median cleft almost closed, with edges in contact. Antennal scale more than 3 times as long as its greatest width..... *P. roseum* G. O. Sars 1870 (W. M. Tattersall (7), Fig. 46)

Erythrops G. O. Sars 1869

Single species found in the area..... *E. erythrophthalma* (Goes) 1864 (Tattersall and Tattersall (8), Fig. 41)

Meterythrops S. I. Smith 1879

Single species found in the area..... *M. robusta* S. I. Smith 1879 (W. M. Tattersall (7), Fig. 35)

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NEMATODE PARASITES FROM VERTEBRATES TAKEN ON LAN YÜ, FORMOSA

I. NEMATODES FROM RATTUS RATTUS[1]

BETTY J. MYERS AND ROBERT E. KUNTZ[2]

Abstract

Capillaria sp., *Globocephalus* sp., *Gongylonema orientale*, *Heterakis spumosa*, *Nippostrongylus braziliensis*, *Protospirura muricola*, *Rictularia tani*, and *Syphacia* sp. were recovered in this survey of the nematode parasites of 80 *Rattus rattus*.

As a part of the biological and geomedical study programme on Taiwan and countries of southeast Asia, an expedition was organized for a short period of investigations on Lan Yü, a small, little-known island 45 miles east of the southern tip of Formosa. This island, due to changing relationships with outsiders, has been recognized on various maps as Botel Tobago, or Koto-sho (by the Japanese), as Lan Yü (by the Chinese), and currently as Orchid Island by westerners. This group of investigators and technicians, designated as the U.S. Naval Expedition to Lan Yü, spent approximately three weeks on the island to permit medical studies of the Yami tribe of aborigines and to make investigations on the parasites of man and animals.

This paper is one of a series based upon the collection of helminths obtained by the examination of approximately 500 hosts on Lan Yü during the month of March 1959.

Materials and Methods

Most of the hosts were taken alive, that is, caught in traps, in nets, or with the aid of the indigenous population. Most of the birds were shot but were examined within 2 to 4 hours after death. A few hosts taken during the last 2 days on the island were transported to the Taipei laboratory for examination. The viscera were removed and each system was examined separately with the aid of a dissecting microscope during and after maceration of tissues with small forceps and scissors. Subsequent examinations were made after tissue had been shaken in a capped bottle with several changes of fresh water. After cleaning, the nematodes were killed by quick immersion in hot water. They were immediately transferred to FAA (formalin, acetic acid, and alcohol) fixative. After 5 to 15 hours in fixative the helminths were transferred to vials with 70% alcohol plus 2% glycerine.

[1]Manuscript received April 20, 1960.
Contribution from the Institute of Parasitology, McGill University, Macdonald College P.O., Que., Canada, and the U.S. Naval Medical Research Unit No. 2, Taipei, Taiwan (Formosa). The opinions and assertions contained herein are those of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service (United States) at large.
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Results

Eighty rats contained identifiable nematodes as detailed in the following list. Of these, the most interesting was the finding of *Globocephalus* sp. in five of the rats. Unfortunately, only females were recovered, thus making it impossible to assign it to a species. The most common nematode found was *Nippostrongylus braziliensis*, which occurred in 31 rats, while the second most common was *Gongylonema orientale*, which occurred in 16. *Rictularia tani* was found in nine, *Protospirura muricola* in five, and immature *Capillaria* sp. in two. Surprisingly, *Heterakis spumosa* and females of *Syphacia* were each found in a single rat.

Parasites

Host: *Rattus rattus*

Capillaria sp. (immature)
Glopocephalus (females only)
Gongylonema orientale Yokogawa, 1925
Heterakis spumosa Schneider, 1866
Nippostrongylus braziliensis (Travassos, 1914) Travassos and Darriba, 1929
Protospirura muricola Gedoelst, 1916
Rictularia tani Hoeppli, 1926
Syphacia sp. (females only)

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THE PREY OF THE SPIDER LINYPHIA TRIANGULARIS (CLERCK) (ARANEAE, LINYPHIIDAE)[1]

A. L. TURNBULL

Abstract

In a study of the natural foods of the spider, *Linyphia triangularis* (Clerck), a weekly 3-hour watch of 50 webs was kept from May 1 to October 15. A total of 581 insects representing 153 species entered webs during the observation periods. Most of these were represented by very few individuals, and more than half of the spiders' diet was supplied by about 20 species of prey. Most of the prey were winged adults. Most of the species were present in the community in the adult stage for a short time only. Thus over the season the spider exploited a constantly changing complex of prey species. At any one time the spider relies on a very few species for most of its food. Of all the insects in the community, only those with certain characteristics of distribution, morphology, and behavior are available to the spiders. Suitable characteristics occur in a wide range of distantly related species; thus the spider is not restricted in its prey to any taxonomic group. From the insects that enter the webs the spider exercises some selection. There is a strong suggestion that new or strange species entering a web tend to be rejected on their first few entries, but if they continue to enter they will eventually be accepted.

Introduction

Beyond the fact that most spiders are polyphagous predators, little is known about their feeding habits, and any preferences or selectivity they may exhibit are largely matters of conjecture. Savory (17) stated: "Spiders will eat all kinds of flies, as well as wasps, bees, ants, beetles, earwigs, butterflies, moths, harvestmen, and woodlice, and other spiders whenever the opportunity occurs . . . they show no trace of discrimination". On the other hand Bristowe (4) said: "I have known for many years that a host of invertebrates were rejected by spiders . . . discrimination and preference for certain insects is shown . . .".

There are many published field records indicating that a wide range of animals are captured by spiders (N. Abraham (2); H. C. Abraham (1); Cuthbertson (6); Emerton (8); Hingston (10); Lorando (14); Fluke (9); Tothill *et al.* (19); Hobby (11, 12); Bristowe (4); Denis (7); Pratt and Hatch (16); Le Gros (13); Newstead (15); Broadhead (5)). Feeding tests with caged spiders also indicate that a wide range of animals are acceptable to them (Shelford (18); Bisling (3); Bristowe (4); Turnbull (20)). These observations lend support to Savory's views. Bristowe, however, showed that a large number of animals are rejected by many spiders apparently because of tastes, odors, or other undesirable features. This study of food consumption by the web spider *Linyphia triangularis* (Clerck) suggests that neither of these contradictory views is completely right, and an alternative hypothesis is advanced.

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Contribution from the Entomology Research Institute for Biological Control, Research Branch, Canada Department of Agriculture, Belleville, Ontario. From a thesis submitted for the degree of Doctor of Philosophy at Oxford University.

The Life and Habits of Linyphia triangularis (Clerck)

L. triangularis is a sedentary, web-building spider. The adults mature in the autumn and the females lay about 30 eggs in one or two flat, roughly triangular egg sacs that are attached to the undersurface of a leaf. When the leaves fall the egg sacs are carried with them and spend the winter in the litter layer under trees and shrubs. The spiderlings hatch in late spring, and following a short dispersal period, each constructs a web on a suitable shrub or tree. Unless seriously disturbed, the spider seems to remain close to the original site for the remainder of its life. The first tiny web is expanded as the spider grows. Where the density of the species is high, adjacent webs may join and form a virtually continuous mass of silk over large areas of foliage.

The web of *L. triangularis* consists of a horizontal sheet of densely woven silk suspended from above by a maze of long, semivertical lines, and anchored below by a few, short, stout lines. The spider hangs inverted below the sheet. Insects flying over the sheet blunder into the maze of suspension lines and either recover their balance and fly on, become entangled in the lines, or tumble to the sheet below. There is no adhesive material in a linyphid web, and potential prey insects quickly escape unless attacked immediately. Non-flying insects occasionally become entangled while crawling over foliage that lies within the margins of the web, and occasionally they tumble from overhanging foliage onto the sheet.

The effective range of perception of *L. triangularis* is limited by the dimensions of the web. Though this spider has the normal complement of eight eyes, eyesight plays little part in the detection and location of prey. Prey in the web are located by vibrations and tensions in the web lines caused by prey movements; a motionless prey cannot be located by the spider.

Study Area and Method

The study was conducted in a mixed deciduous stand in Wytham Wood, Berkshire, England. This wood is traversed at intervals by a number of rides about 10 to 12 ft wide that are kept clear of woody plants. One of these rides was bordered by a dense stand of grasses and other herbaceous plants backed by an almost solid wall of bramble (*Rubus* sp.) about 3.5 to 4 ft high. Webs of *L. triangularis* were abundant in this border vegetation and were easily examined from the cleared pathway. On each observation day 50 webs were marked with small tufts of white cotton, and a 3-hour watch was kept by a constant patrol back and forth along the path. Each of the 50 webs was visited about once every 10 minutes. Watches were conducted once a week from May 1 until October 15, i.e., throughout the developmental period of the spider. Any insect observed entering a web during an observation period was scored according to whether it was accepted or rejected by the spider. Insects that struck the web but maintained their balance were not scored, as the spider had no opportunity to select from these. If a spider failed to respond to the presence of an insect caught in the web, or retreated from it without attacking, the insect was scored as rejected. If the spider

attacked but abandoned the attack after touching or tasting the insect, it was again scored as rejected. All rejected insects readily escaped from the web. If the spider attacked and the attack was sustained, the insect was scored as accepted though it might subsequently have repulsed the attack and escaped.

Rejected insects were captured and stored for future identification as soon as the rejection became apparent. Accepted insects were taken from the spider as soon as a sustained attack was established. Many of the insects taken were badly damaged before they were recovered, which often made their identification difficult. At the same time notes were kept on the general behavior of insects in the vicinity of the web, and of any reactions of the spiders to the presence of insects near the webs.

All observations were made between 1.00 and 4.00 p.m., G.M.T. The insects noted in this study were therefore day-flying species only. A similar study conducted at night would probably reveal many additional prey species.

Results and Discussion

Web-building spiders do not seek out their prey; other than by building their webs in appropriate sites spiders are unable to influence the kinds or numbers of prey that come to them. The effective contact between predator and prey is established by the entry of a prey into a web, and this is a result of prey movements beyond the control of the spider.

In this study 581 individuals representing 153 species of insects were observed entering webs of *L. triangularis*. The distribution of the individuals among the 153 species was as follows:

Individuals per species	1	2	3	4	5	6	7	8	11	12	14	18	20	23	26	27	43	
Species	70	23	16	9	6	5	5	6	5	1	1	1	1	1	1	1	1	153
Web entries	70	46	48	36	30	30	35	48	55	12	14	18	20	23	26	27	43	581

This table shows that most of the individuals entering the webs consisted of a small proportion of the species, e.g. more than half the total entrants were supplied by only one-eighth of the species. It is upon these few species, then, that the spider must depend for the bulk of its food. Regardless of its preferences, the spider must feed on the prey that are available to it, and, unless large surpluses are available, it must feed most frequently on the species of prey that are available in greatest abundance. Thus the factors that determine what kinds of prey, and how many of each kind, enter spider webs are of first importance in a consideration of the kinds of animals eaten by spiders.

Before an insect can enter a spider web it must move into the vicinity of a web, i.e., it must approach it. Not all insects that approach a web enter it, and the factors that cause an insect to enter a web may differ from the factors that cause it to approach the web. For the purpose of this discussion, therefore, a distinction will be made between the act of approaching a web and the act of entering a web. The term "approach" will be reserved for those activities of insects which cause them to come close enough to be able to detect the presence

of a web: for some insects this may be a distance of several inches; for others, actual contact with the web may be required. The term "entry" is used here to mean the actual penetration of the web by an insect.

Insects that Approach L. triangularis Webs

L. triangularis webs are stationary obstacles. Insects must move about if they are to approach them. Other things being equal, therefore, the insect that is most mobile has the greatest chance of approaching a web. The same generality applies to a species of insects, but the mobility of a collective group such as a species is the product of the distance each individual of the group moves and the number of individuals making up the group. For example, if there are 100 individuals of species A and each individual moves 10 meters, the total mobility of the species is 1000 meters; on the other hand if there are but 10 individuals of species B and each moves 100 meters, the total mobility of B is the same as that of A, and, if all other things are equal, both species will have an equal chance of approaching a web.

The above proposition can be true only if insect movements are random. Then all webs, no matter where they are situated in the community, will have an equal chance of being approached by any insect. But insect movements are not random. Some insects, for instance, crawl or walk, some hop or jump, and some fly or drift on air currents. Two insects, one of which crawls and one of which flies, obviously do not have equal chances of approaching a web suspended 6 feet above the ground. In this study, of the 581 insects removed from *L. triangularis* webs, 532 were winged adults, 42 were jumpers (froghoppers and leafhoppers), and only 7 were walkers (4 immature *Stenodema lavigatum* (L.), and 3 immature *Phytocoris tiliae* (F.), both Miridae, Heteroptera). For a period of several weeks in early summer immature Heteroptera were among the most abundant and active of the insect groups in the community but, because their mode of locomotion confined them to parts of the community not occupied by *L. triangularis* webs, they rarely approached these webs and rarely entered them. Many other crawling or walking insects, such as larvae of lepidopterous defoliators (*Tortrix viridana* (L.), *Operophtera brumata* (L.)) were also abundant in the community, but were excluded from the webs for the same reason.

But even within those parts of the community that are physically available to them, insects do not move at random. Insect movements are induced by stimuli, and are thus directed towards certain parts of the community. Individuals of one species tend to respond to a given stimulus similarly to other individuals of the same species, and differently from individuals of all other species. Thus there will tend to be a measure of segregation of species in the community, and certain species will move in certain areas more frequently than other species.

There are undoubtedly many factors that influence the siting of webs by a particular species of spider, most of which are unknown. But a spider web is not a self-supporting structure and can only be built where a suitable scaffold exists to support it. As webs vary greatly in form and method of construction,

the types of scaffolding required for their support must vary also. For instance, a micryphantid web can be built on the ground surface, with small irregularities of the soil sufficing to support it; other webs, such as those of argiopids and linyphiids, must be suspended from some external, elevated structure. Argiopid webs are primarily two-dimensional and require only two-dimensional support; linyphiid webs are three-dimensional and require a three-dimensional scaffold. Still other types of webs require other forms of support: some theridiid and dictynid webs need internal support, agelinids require a crevice, preferably one with walls, and so on. Moreover, within these broad, family types of webs are a large variety of subtypes, each of which, no doubt, is most successfully built on a certain fairly specific kind of site. On the basis of web architecture alone, therefore, it is evident that all sites are not equally available for all types of webs. Many other factors, such as humidity, amount of sunlight, air currents, height above ground, etc., probably also influence the choice of site, and each of these factors will tend to further restrict the kind of places where each sort of web will be found.

Suitable sites for a particular kind of web will occur most frequently in fairly clearly definable parts of the community. This is well known to spider collectors, who soon learn what parts of a community should be searched to find a certain kind of spider. *L. triangularis* webs, for instance, are mainly found in shrubby vegetation of the field layer, i.e. that structural layer of a deciduous woodland community above the ground zone and below the tree canopy. *L. triangularis* webs, of course, are not confined to this part of the community, but more of them will be found in such places than elsewhere (21).

Because each kind of insect tends to move most frequently in certain restricted parts of the community, and because each sort of web likewise tends to occur most frequently in certain restricted parts of the community, a particular kind of web will be approached most frequently by those insects that normally move in the parts of the community occupied by this type of web, and insects that normally move in other parts of the community will rarely, if ever, approach such webs.

Insects that Enter the Webs

Many of the insects that approach *L. triangularis* webs do not enter them. Some are clearly able to avoid webs. In this study, strong-flying insects were frequently seen to approach a web of *L. triangularis*, hover for an instant at a distance of an inch or so, then carefully thread their way through the extensive maze of suspension lines and emerge unscathed from the opposite side. Other insects were seen to back off and fly around webs. Either feat requires keen perception and a high degree of flight manoeuvrability, attributes not equally possessed by all insect species.

The stimuli by which insects detect spider webs are unknown. Sight probably plays a dominant role. There is a suggestion that some flies tend to avoid lines that cross their field of vision, and a preference for spaces between lines may be shown (Tretzel, personal communication). But the lines of a spider's

web are often almost invisible to human eyes. Whether insect eyes can resolve such delicate images is questionable, so the possibility that sense organs other than eyes may be involved cannot be ruled out.

Perception of a web is of little value unless it results in an avoiding action. The efficiency by which an avoiding action can be taken depends on the flight characteristics of the species, and these vary widely. The higher Diptera and Hymenoptera are probably the most adroit flyers. Many of them can hover motionless in mid-air, rise or fall vertically, or even reverse direction at will. While not completely invulnerable to the hazard of spider webs, these insects are very bold and make no perceptible effort to shun the vicinity of webs. Such flies as syrphids, for instance, were commonly observed close to *L. triangularis* webs, but very few were ever caught in a web. On the other hand many strong-flying Homoptera and Coleoptera, as well as some flies such as Bibionidae, seem to fly in long curving arcs and are incapable either of perceiving webs, or of altering the trajectory of their flights to avoid webs. Jumping insects similarly have little control over the trajectories of their leaps and are unable to avoid webs. Leafhoppers and froghoppers constituted the chief group of jumping insects encountered in this study, and they were common among the species collected from *L. triangularis* webs.

There are many insects that are not strong flyers. These include many nematocerous flies, small gall-forming and parasitic wasps, aphids and their allies, Microlepidoptera, etc., that are more or less at the mercy of air currents. Even on relatively still days when winds did not exceed 4 to 5 m.p.h. many of these insects were carried into *L. triangularis* webs by air currents. These are the insects most commonly found in *L. triangularis* webs, particularly early in the season when both the spiders and their webs are small.

Thus far this discussion has not dealt with changes that occur in the community with the passage of time. But it must be apparent that not all potential prey species are available to the spiders at all times. In this study a total of 153 species of prey were taken from *L. triangularis* webs during weekly 3-hour observation periods distributed over a season of 6 months. But no more than one-fifth of these species were ever available to the spiders at any one time: the mean number available in any one period was 14 ± 1 species, or less than $\frac{1}{10}$th of the species available in the entire season.

There are at least two obvious factors that restrict the number of prey species available to a spider at a particular time: the changing powers of the spider web to intercept and hold different sizes of insects, which is a reflection of the growth of the spider and its web; and the seasonal changes in the kinds and stages of insects present in the community, which are a reflection of the life-histories of the potential prey species.

From the newly hatched spiderling to the mature, gravid female, the weight of *L. triangularis* may increase over 100-fold (Turnbull, in preparation). The size and strength of the web increases at least proportionally to the growth of the spider. The initial web of the hatchling *L. triangularis* consists of a few delicate lines supporting a gauzy sheet somewhat less than 1 in. in diameter.

TABLE I

Number and proportion of each size class of prey taken from *L. triangularis* webs in a 3-hour period once each month

Size class of prey (length × width in mm)	May		June		July		Aug.		Sept.		Oct.	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
0.00– 1.99	19	68	3	19	4	11	4	13	3	12	2	8
2.00– 9.99	9	32	10	62	15	42	13	41	8	31	6	23
10.00–19.99			3	19	14	39	6	18	6	23	9	35
20.00–29.99					1	3	6	18	6	23	4	15
30.00					2	5	3	9	3	12	5	19
Total	28	100	16	100	36	100	32	99	26	101	26	100
Mean prey size (length × width in mm)	2.26	±0.25*	5.91	±0.86	10.85	±1.41	13.96	±2.23	16.07	±2.43	19.07	±2.84

*Standard error of mean.

The sheet of a mature spider's web usually has a mean diameter of well over 1 ft, and is suspended by a maze of hundreds of lines. The larger the web, the larger and stronger are the insects it will hold. The gradual increase in size of prey found in *L. triangularis* webs as the season progresses is shown in Table I.

All of the insects that were removed from *L. triangularis* webs on the second observation period of each month were divided into size classes based on the product of their length and width measured in millimeters. It may be seen that in May, when the spider and web are smallest, the prey is also small. As the season advances, small prey continue to come to the webs, but larger and larger classes of insects are added each month until July. Thereafter, until October, the proportions of larger size classes increase continually. The mean size of prey for each month is also shown in the table, and it is apparent that prey size increases steadily over the season.

In the spring and early summer, therefore, the larger insects that may be in the community are not available to the spider. In late summer and autumn, however, size ceases to be a factor that governs the availability of prey, and all size classes of insects, with the possible exception of the very largest, are equally available to *L. triangularis*.

Though some species of insects have overlapping generations with all life-stages represented in the population throughout much of the summer, a great many species have discrete generations with most of the individuals passing through the same stages of development at the same time. In populations of the latter type each stage of the insect is present in the community for a limited time only. Insects in the adult stage constituted over 90% of the prey of *L. triangularis* observed in this study. Most of the prey species were therefore available to *L. triangularis* only for the limited time they were in the adult stage.

In this study insects coming to *L. triangularis* webs were observed at weekly intervals. Prey species observed on a single observation day were considered to be present in the community as adults for 1 week only; those observed on two consecutive days for 2 weeks, and so on. A frequency distribution of the 153 species based on the length of period over which they were observed entering webs follows:

No. of species	80	19	12	13	5	5	5	1	5	2	2	1	1	1
No. of weeks species were observed entering webs	1	2	3	4	5	6	7	8	9	10	14	18	20	21

Though a very few species came to the webs for most of the season, over 80% persisted for less than 4 weeks. As the season is at least 22 weeks long, few species of prey can be available to the spiders for all of this period.

This is apparent when we examine the species of insects that were taken from the webs at various times throughout the season. Figure 1 shows the relative abundances of the broad groups of insects collected from the webs on each observation day.

Small Hymenoptera, mainly Cynipidae, were dominant among the species that came to the webs until the end of May. In early June, however, the numbers of Hymenoptera declined, and virtually none were seen in the webs until July, when a few braconids and ichneumonids were found. Various larger Hymenoptera continued to occur in moderate numbers throughout August. From September to mid-October species of Hymenoptera increased in numbers sharply until they constituted about 38% of the total catch.

Species of Diptera were taken from the webs all summer. In early spring Nematocera constituted 18% of the insect species that entered *L. triangularis* webs, but by June, Diptera species, still mainly Nematocera, comprised a full 80% of the total prey. In early July the numbers of Diptera declined somewhat, but in August they rose again. In the autumn months higher Diptera began to appear in the webs in increasing numbers and eventually became equally abundant to the nematocerous species.

Though immature Heteroptera and Homoptera were abundant in the community from May, few were found in the webs until late June and early July when species of these groups began to mature. Bugs were very abundant and accounted for the majority of the insect entries into *L. triangularis* webs in July. By mid-August the peak abundance of bugs passed and the number of entries by this group declined steadily until early September, when they virtually disappeared from the webs.

The numbers of Lepidoptera and Coleoptera were never great, but individuals representing these orders occurred from May to September. The numbers of Coleoptera increased somewhat in late October. Individuals from other orders occurred throughout the season but their numbers were insignificant compared to the numbers of Hymenoptera, Diptera, and Hemiptera.

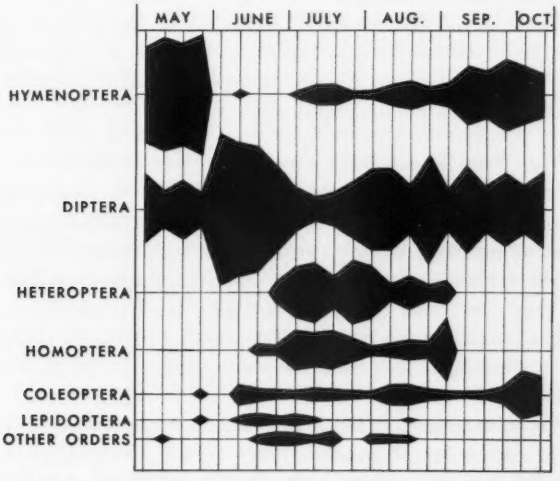

FIG. 1. The relative abundances of insect orders coming to *L. triangularis* webs throughout the season of spider activity.

When an insect approaches or enters a web of *L. triangularis*, the chances of it touching a web line are strongly influenced by its body form. Nematocerous flies with slender abdomens, long narrow wings, and attenuate appendages, for instance, have difficulty in manoeuvring through a maze of lines without touching one of them. Moreover, when it touches one line, such an insect is liable to become seriously upset, and its struggles cause it to become entangled in the many fine threads nearby. It may thus be delayed sufficiently for the spider to locate and attack it. Higher forms of flies with more compact bodies and shorter, stouter wings and legs have less difficulty in avoiding lines and are less likely to become ensnared in many lines. Long spines add to the hazard of entanglement in web lines, and a hairy or spiny integument greatly increases the probability of ensnarement once a line is touched. In spite of their superior manoeuvrability, higher dipterans are vulnerable for this reason. Many species of Hymenoptera, Hemiptera, and, particularly, Coleoptera possess smooth polished surfaces that offer little purchase to the ensnaring silk, and such insects often touch many web lines with impunity. Thus the Coleoptera that frequently blunder into webs are seldom seriously impeded and usually fly on unobstructed. Large, powerful insects also are frequently able to pass through a web without serious difficulty. Some, such as heavy-bodied beetles, are able to crash right through a stopping maze; others, such as large wasps, bumble bees, and moths, are temporarily checked but thrash about with such vigor that the web is rapidly destroyed and the spider often retreats. The antithesis of this situation is found with those small, weak-flying insects that are carried into webs by air currents. Some of these are so small, and their struggles so feeble, that the spider fails to attack. Such small insects are unlikely to encounter more than one line at a time, so they rarely become seriously entangled and frequently escape.

Thus, of the insects that enter *L. triangularis* webs, those that possess certain characteristics which render them vulnerable to ensnarement in the web are most liable to be attacked by the spider, and the prey of the spider must necessarily be drawn mainly from those species.

Selection of Prey from Insects that Enter L. triangularis Webs

Thus far in this discussion I have suggested that of all the insect species present in a community, only a few with certain characteristics of distribution, behavior, and morphology enter *L. triangularis* webs repeatedly and are thus available to the spider in quantity. The factors that determine the availability of potential prey species to the spider are usually characteristics of the prey over which the spider has no control. Among the restricted group that enter webs, however, the spider may exercise any selective or discriminative powers it may possess.

Of the 153 species of insects that entered *L. triangularis* webs in this study, 3 species, accounting for 12 entries (mean of 4.0 entries per species), were rejected by all spiders in whose webs they were observed; 117 species, accounting for 296 entries (mean of 2.5 entries per species), were accepted by all

spiders in whose webs they were observed; and 33 species, accounting for 273 entries (mean of 8.3 entries per species), were accepted by the spiders on some occasions and rejected on others. That is to say, 150 of the 153 species of insects that entered the webs were acceptable to the spiders on some occasions. But a total of 103 of the individuals that entered the webs were rejected, indicating that some measure of discrimination is exercised by *L. triangularis* on at least some occasions.

It may be significant that the species of insects observed most frequently in the webs were those toward which the spiders exercised both of the possible alternatives, acceptance and rejection; those species that were observed only on a few occasions were consistently either rejected or accepted. Several species that were rejected on four or more consecutive occasions were accepted on other occasions; similarly species that were accepted on four or more occasions were rejected on other occasions. Thus we cannot escape the suspicion that much of the unanimity of acceptance and rejection of certain prey species observed in these spiders was more apparent than real, and is, in fact, a product of an inadequate number of observations for these species. On the bases of this evidence, therefore, it would be dangerous to claim that any insect species was consistently unacceptable to *L. triangularis*, or that any species was consistently acceptable. We can only conclude that most species of insects that enter *L. triangularis* webs are acceptable to the spiders on at least some occasions, but many species are likely to be rejected on other occasions.

The physiological state of a spider at the moment a potential prey enters a web probably has a great deal to do with the acceptance or rejection of the prey by the spider: a hungry spider may attack a distasteful prey; a satiated spider may reject a desirable prey. Many other factors, such as imminence of a molt, alarm, time of day, and intensity of light, moisture, temperature, or wind, may produce similar effects. If feeding by a spider is inhibited or stimulated only by physiological factors, however, we would expect all prey species to be rejected during periods when an adverse physiological condition existed, and all species to be accepted during a period when physiological factors were favorable. But spiders were often observed feeding freely on certain species while other species were rejected. This would seem to indicate the existence of a real preference for the accepted species over the rejected species. On other occasions, however, the species that originally seemed preferred were rejected, and ones that were previously rejected became preferred. Thus the relative preferences for certain species are not constant and seem to change with time.

The 33 species that were observed to be accepted by *L. triangularis* on some occasions and rejected on others provide us with an opportunity to examine the sequences of acceptance and rejection. This is shown in Table II.

The observation days in this table are at weekly intervals, and represent the first, second, third, etc., days that each species was observed in a web regardless of what calendar day these were. The prey species are divided into two classes based on whether the first individual of each species observed in a

web was rejected (class I) or accepted (class II). The numbers of species and individuals in each class are given, as well as the percentages of individuals that were rejected on each day.

TABLE II

Proportion of individuals that were rejected by *L. triangularis* on the first and subsequent observation days that each species of prey were observed in a web. Observation days were at weekly intervals

Class of prey		Observation day									
		1	2	3	4	5	6	7	8	9	10
I. Prey species of which the first individuals observed in the webs were rejected	Number of species	25	19	15	9	8	5	3	3	3	0
	Number of individuals	52	57	38	26	18	11	3	6	5	0
	% of individuals rejected	75	28	26	16	22	27	0	0	0	0
II. Prey species of which the first individuals observed in the webs were accepted	Number of species	8	6	5	4	3	2	1	1		
	Number of individuals	9	10	10	10	5	2	1	2		
	% of individuals rejected	0	40	30	0	60	50	100	100		
Total class I and class II	Number of species	33	25	20	13	11	7	4	4	3	0
	Number of individuals	61	67	48	36	23	13	4	8	5	0
	% of individuals rejected	64	30	27	11	30	31	25	25	0	0

Of the 33 potential prey species, in 25 the first individual observed entering a web was rejected, and 75% of all the individuals in this class were rejected on day 1. In only nine species were the first individuals accepted. As eight of these nine species were represented by a single individual and the remaining species by two individuals, it is not surprising that no individuals in this class were rejected on day 1. In class I there was a large drop in the percentage of individuals rejected on the second day species continued to come to the webs, but from the second to the seventh day the percentages of rejections remained fairly constant. The few species that continued to come to the webs for more than 7 days are represented by too few individuals to supply a reliable estimate of the proportion of individuals rejected. In class II the number of rejections increased sharply between the first and second days, but thereafter fluctuated so widely that no trend could be established. But, though the species in class II do not seem to follow the same trend as those in class I, the general trend remains apparent when the two classes are summed.

These data, therefore, seem to indicate that for many species of potential prey, the first individuals to enter a web are less attractive to the spiders than individuals that enter later; that is to say, a species that is unfamiliar to a

spider is less likely to be attacked than a species with which the spider has had previous experience. An extension of this hypothesis is that the spiders will prefer to feed upon the species with which they are most familiar, i.e. the species that at a given time are most abundant in the webs.

This hypothesis, however, is based on periodic observations which covered somewhat less than 1.4% of the active life of the spiders. In addition, all observations were made at the same time of day. What happened at other times of the day, or on days between observation periods, in unknown. Moreover, the data upon which this hypothesis is based includes only about 20% of the prey species observed entering the webs, those that entered frequently enough to allow the spiders to exercise alternative choices. The interpretation of these data, therefore, can hardly be considered conclusive, but do give grounds for more detailed analytical studies. These are in progress.

Conclusions

L. triangularis is evidently a truly polyphagous predator. It is able and willing to feed on a wide range of species; in fact there is no evidence to demonstrate that it will not feed on any species available to it. Bristowe (4) listed many insect species that were rejected by various spiders including *L. triangularis* (= *L. montana* Linn. of Bristowe). But in view of the alternative acceptance and rejections of certain prey observed in the present study, Bristowe's feeding tests were inadequate to provide conclusive demonstrations of unacceptability. A single rejection, or even a number of consecutive rejections, merely demonstrate that at the time of the tests the prey offered were not desired by the spider. The reasons may be many: the spider may be physiologically or psychologically unprepared to feed; the manner of offering the prey may alarm the spider; or at the moment of offering the spider may find a particular prey distasteful or may not recognize it as a potential food. We have seen in the present work that the species of prey acceptable by *L. triangularis* seems to vary from time to time, and there is a suggestion that familiarity with a species may be important. If this is true, a strange or unusual prey suddenly thrust upon a spider is unlikely to be accepted though there is nothing inherently objectionable about it.

Bristowe recognized that the apparent revulsion of spiders to certain prey species was not a constant characteristic, but the acceptance by a spider of a species that he had labelled "distasteful" Bristowe attributed to hunger on the part of the spider: "A hungry spider is liable to accept an insect which it will reject when well fed, indicating thereby that sometimes a spider's distaste is relative and not absolute." Some species may be more or less distasteful to *L. triangularis*, and this factor may have a bearing upon which of two equally available species it will choose to feed upon. But if this is true the distasteful characteristics are not obvious to a human observer. Some of the bugs that were readily accepted by *L. triangularis* emitted odors very disagreeable to me. Yet on occasion these species seemed to be preferred over equally available but less malodorous species.

But the willingness or ability of *L. triangularis* to feed upon various species appears to be of secondary importance. The only prey from which *L. triangularis* can select are those that enter its webs, and whatever the spider's preferences may be, it is forced to secure its food from the species that enter the webs in sufficient numbers to satisfy its needs. This fact may obscure preferences that the spider might exhibit if it always had a free choice from a number of prey species all of which were equally and adequately abundant.

There are a number of conditions which must be fulfilled by a potential prey species before individuals of the species can be available to *L. triangularis* in significant numbers. The species must be highly mobile as only insects which move can approach or enter a web; this condition eliminates sessile or sedentary species. The normal activities of the species must bring it into those parts of the community occupied by *L. triangularis* webs; this condition eliminates most walking or crawling forms, as well as those flying forms whose normal flight activities are directed to parts of the community other than the shrubby vegetation of the field layer. The species must be unable to avoid coming into contact with a web if it should approach one; this condition eliminates species with acute perceptive senses and a high degree of flight manoeuvrability. The species must be susceptible to ensnarement by the lines of the web; this condition eliminates very powerful animals, very small animals, and animals with smooth, polished integuments and compact bodies free from attenuate appendages or spines. It is not claimed that these conditions eliminate any species absolutely. The occasional individual of practically any distribution, habit, or form may become ensnared in a web of *L. triangularis*, but the numbers of individuals not fulfilling the above conditions will be few compared to the numbers of individuals that do fulfil them.

Bearing these conditions in mind, let us postulate an ideal prey for *L. triangularis*. Size considerations dictate that it should be an arthropod, and as it must fly it can only be a winged adult insect. It must be attracted by some stimulus that arises from within the shrubby vegetation of the field layer, be it microclimate or some product of the plants or animals that occur there. Although it must be highly mobile it should not be a strong or adroit flyer. It must have poor perceptive senses, and preferably a slender, elongate body, with long wings, attenuate appendages, and an abundance of hairs or spines. Now there are any number of unrelated insect species that conform to most of these specifications; some may be deficient in one or more character but especially developed in others. It is the degree to which these characteristics are possessed by a species that will determine the real "preference" of *L. triangularis* toward it, i.e. the relative numbers of the species that will be eaten by the spider. Thus the food "preferences" of *L. triangularis* are unlikely to be tied to any particular individual taxonomic class of insects, and it will be futile to attempt to determine any particular species or species group that is preferred by this spider. *L. triangularis* will tolerate a wide range of species

of prey, and the "preferred" species will vary from time to time, and from place to place, depending on the particular species present at the particular time and place.

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A REVISION OF THE GENUS PERGETUS (COLEOPTERA: PEDILIDAE)[1]

MOHAMMAD ABDULLAH

Abstract

Casey (1895) erected a new genus *Pergetus* on the basis of *Eurygenius campanulatus* Leconte, 1874. In this work the genotype has been redefined on the basis of both male and female characters, and limits of the genus have been established. Additional records on distribution are also included.

Introduction

The original description of *Eurygenius campanulatus* as given by Leconte (4) is very short and rather incomplete. Subsequent erection of the genus *Pergetus* based on this species by Casey (3) further necessitated a revisional study.

The object of this paper is to redescribe the genotype on the basis of both male and female characters, to present additional data on geographical distribution, and to comment on the systematic position of the genus.

Description

Pergetus Casey, 1895, pp. 636–637

Medium-sized. *Vestiture* dimorphic, body clothed with irregular pubescence. *Eyes* entire, finely faceted, separated by more than twice their width above. *Tempora* well developed. *Antennae* filiform with the terminal joint abruptly attenuate at the middle. *Maxillary palpi* four-segmented, first segment smallest and subtriangular, last segment subtriangular, excavated on inner side, as large as the preceding segments combined. *Labium* small with mentum subrectangular, rounded on sides. *Neck* hairy, wide. *Pronotum* strongly campanulate with deep median canaliculation. *Claws* with lobular membranous empodium. *Wings* with anal cell closed. *Abdomen* with fifth sternite slightly emarginate in male, rounded to subtruncate in female. *Male genitalia* with parameres finely and sparsely spined, aedeagus longitudinally serrate at apex. *Female genitalia* hairy on apex.

Pergetus campanulatus Leconte, 1874, p. 69; Casey, 1895, pp. 636–637

Male.—Length 8.3 mm. *Width* 2.6 mm. *Color:* pale brown to black, maculose. *Head* as long as broad, not wider than prothorax, black, densely clothed with irregular silvery pubescence, epicranial and frontoclypeal sutures obliterated, clypeolabral suture prominent, vertex broad. *Eyes* large, laterally bulging, entire or only feebly sinuate, separated by more than twice their width above, black. *Antennae* rufous, filiform, 11-segmented: first segment large, obconic,

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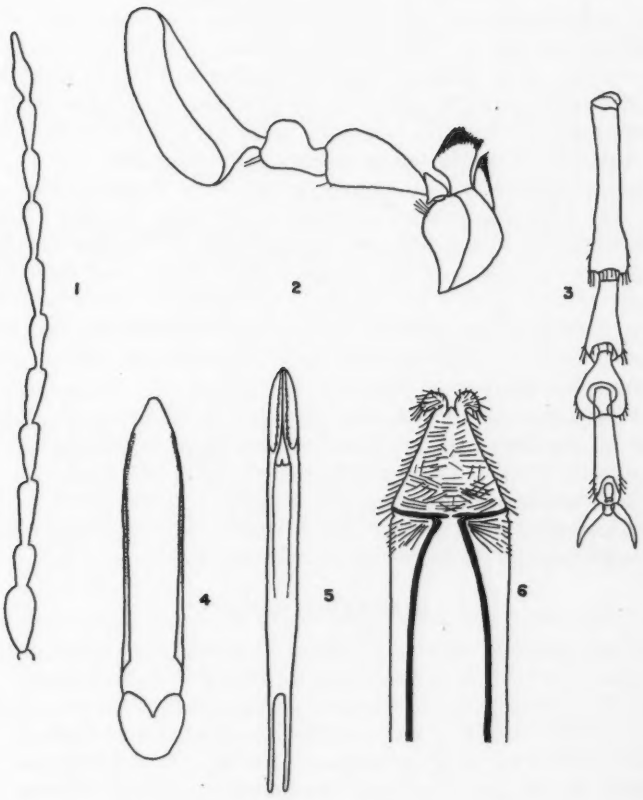
Contribution from the Department of Entomology, University of Illinois, Urbana, Ill.

more than twice as long as wide, second segment half as long as first, last segment longer than 10th, abruptly tapering beyond middle (Fig. 1). *Labrum* sparsely punctured, about twice as broad as long, apex fringed with long hairs. *Mandibles* nearly twice as long as broad. *Maxillae* sparsely hairy, galea much bigger than lacinia. *Maxillary palpi* large, four-segmented: first smallest and subtriangular, second twice as long as third, fourth as large as preceding three segments combined, broad, subtriangular, excavated on inner side laterally (Fig. 2). *Labium* small, mentum subrectangular but bulging laterally; labial palpi three-segmented, first two segments as long as broad, last segment largest, triangular. *Neck*: black, hairy, about half as wide as pronotum. *Prothorax* black, hairy, punctulate, about as long as wide, strongly campanulate, sides suddenly rounded beyond the middle, then narrowed, margined at base, median canaliculation deep, dividing pronotum into two distinct halves. *Mesepisterna* meeting in front of mesosternum. *Metasternum* hairy but not spined. *Scutellum* rounded at apex. *Elytra* pale brown to black, punctate, pubescent, more than twice longer than wide, sides parallel becoming rounded at apex. *Legs* pale to black, densely pubescent, coxae nearly contiguous, tibia spinulate, tibial spurs long, tarsi 5,5,4. (Fig. 3). *Abdomen* pubescent, fifth ventral sternite slightly emarginate, sixth nearly entire. *Genitalia*: parameres (lateral lobes) slender, finely and sparsely spined (Fig. 4); aedeagus (median lobe) with long basal processes, longitudinally serrate at apex (Fig. 5).

Female.—Length 12.2 mm. *Width* 4 mm. *Antennae* with second segment more than half as long as first. *Scutellum* broadly rounded at apex or subtruncate. *Abdomen* with fifth ventral sternite rounded to slightly truncate. *Genitalia*: valvifers with long spines on apex, especially on sides (Fig. 6).

Type locality.—Vancouver Island, Canada.

Distribution.—Specimens have been examined from the following places: ALBERTA: High River (CAS) 1, Edmonton (CNC) 1. BRITISH COLUMBIA: Agassiz (CNC) 2, Bella Koola (CAS) 1, Burns Lake (INHS) 1, Cranbrook (CNC) 1, Fernie (CAS) 2, Indian River (CAS) 3, Jordon River (CNC) 1, Merritt, Midday Valley (CAS) 3, (INHS) 3, Sugar Lake (CAS) 1, Swift Creek (INHS) 1, Veddan River (INHS) 1. IDAHO: Priest Lake, Coolin (CAS) 1, no locality (WSU) 1. WASHINGTON: Bares State Forest (U.MASS) 1, Baring (CAS) 2, Forks (CAS) 2, Lake Cushman (U.Mich) 2, Lewis River (S) 1, Long Beach (CAS) 1, Longmires Ranie (CAS) 1, Merritt (U.MASS) 1, Metaline Falls (CAS) 1, Monroe (CAS) 10, Mt. Rainier (U. MASS) 2, Northbend (CAS) 22, Olympic, Hoh River (U.MASS) 1, Pullman (CM) 4, Seattle (CAS) 7, (WSU) 1, Spokane (WSU) 1, White Rock (CAS) 1, no locality (CNHM) 2, (CU) 2. OREGON: Cakridge (CAS) 1, Cannon Beach (CAS) 1, Corvallis (CAS) 11, Dayton (U.MASS) 1, Homestead Inn, Mt. Hood (CAS) 1, Hood River (CAS) 1, Klamath Lake (CAS) 1, Mist. Columbia Co. (CAS) 1, Monroe (CAS) 1, Waldport (CAS) 1, no locality (CU) 5, (UOM) 5. CALIFORNIA: Benhomand (S) 1, Lake Tahoe, Bijou (CAS) 3, Carville (CAS) 6, Cole (CAS) 2, Cp. Marwedal (S) 1, Delnorte Co. (CNHM) 6, Derville (CAS) 1, Humboldt Co. (BM) 2, Hydesville (CAS) 2, L. Gatos (CAS) 1, Lassen Co.



FIGS. 1–6. *Pergetus campanulatus* Leconte.
FIG. 1. Male antenna.
FIG. 2. Male maxilla.
FIG. 3. Hind tarsus with claw and empodium.
FIG. 4. Male tegmen, ventral view.
FIG. 5. Male aedeagus, ventral view.
FIG. 6. Apical portion of female genitalia in ventral view.

(CNHM) 2, Mendocino Co. (CAS) 1, Puget Sound (AMNH) 3, Siskiyou Co. (USNM) 3, (CAS) 1, Summit (CAS) 12, Truckee (CAS) 1, Tuolumne Co. (CAS) 1, Wallow Mountains (CAS) 1, Weott (CAS) 1, no locality (AMNH) 1, (CNHM) 1.

Collection date.—April 28 to August 28.

Larvae.—This is apparently the only species in the family Pedilidae in which larvae are known. They are characterized by having annular spiracles and urogomphi with a branch at base (2).

Comparison with Related Genera

Pergetus can be easily distinguished from all other described North American genera of Pedilidae by the following combination of characters: tarsal claws unappendiculate, neck wide, eyes entire, antennae filiform with the 11th segment attenuate at middle, spurs of hind tibia long, tarsal claws with lobular empodium, tempora distinct, maxillary palpi very broad with the fourth segment excavated laterally, and wing with anal cell closed.

Stereopalpus Laferte is most closely related with *Pergetus* from which it differs in the following characters: eyes larger, spurs of hind tibia short, pronotum without a strong median canal, aedeagus with a pair of large backwardly directed spines, and female genitalia robust and more strongly sclerotized.

Retocomus differs in the following characters: eyes narrowly and distinctly emarginate, maxillary palpi less developed, pronotum not sulcate along the middle, and tibial spurs short (3).

Leptoremus Casey is distinct from *Pergetus* as follows: eyes emarginate, separated by less than half their width above, tempora indistinct, antennae serrate, maxillary palpi with fourth segment obliquely truncate, twice as big as third, pronotum without a median depression, claws without empodium, parameres each with a row of large spines laterally, aedeagus sinuously serrate at apex and female genitalia slender without spines (1).

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NEMATODE PARASITES OF VERTEBRATES OF EAST PAKISTAN
VII. CAPILLARIA COPYSCHI SP. NOV.[1]

S. P. GUPTA[2]

Abstract

Capillaria copyschi sp. nov. is described from *Copyschus c. saularis.*

Capillaria copyschi sp. nov.

(Figs. 1–8)

The material available consisted of two male worms, the heads of which were missing, and a number of complete females.

Host: Copyschus c. saularis.
Location: Small intestine.

Description

Body very slender (Fig. 5), covered by a series of cuticular bosses. Oesophageal portion (Fig. 1) shorter and slightly thinner than posterior portion. Vulva near to mid-body just behind junction of oesophagus and intestine, provided with a protrusible funnel-shaped cuticular appendage (Fig. 7), and with the cuticle of the body inflated anterior and posterior to the vulva. Posterior end of female cylindrical and rounded. Anus (Fig. 6) subterminal. Egg barrel-shaped (Fig. 8) and thick; plugs very broad; innermost egg shell bent to form collar; outer shell with reticulation.

Caudal end of male provided with rounded bursalike membrane, supported by pair of L-shaped processes (Figs. 2, 4), each of which bears a terminal papilla. Spicule long, slender (Fig. 5), about 0.01 mm broad surrounded by transversely wrinkled sheath without spines. Proximal end of spicule inflated (Fig. 3) ending in an open funnel more or less curved or bent to one side. Spicule ends in a bluntly rounded tip, somewhat narrowed just before end. Cloacal aperture terminal, surrounded dorsally and on side by small scoop-shaped transparent bursa.

Male.—Maximum width 0.05 to 0.06 mm; width at posterior end of oesophagus 0.04 mm. Distance from posterior end to oesophagus 3.51 to 3.76 mm. Spicule 0.83 to 1.32 mm long, 0.01 to 0.02 mm wide. Sheath 0.1 to 0.37 mm long. Bursa 0.05 to 0.08 mm in diameter.

Female.—Length 10.5 to 12.87 mm, maximum width 0.07 to 0.09 mm; width at vulva 0.06 to 0.08 mm. Length of oesophagus from anterior end 4.5 to 5.15 mm, and from posterior end to oesophagus 4.56 to 5.21 mm. Vulva just behind end of oesophagus. Distance from vulva to oesophageal gland 0.06 mm. Eggs measure 500 to 600 μ by 220 to 260 μ in size.

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Contribution from the Institute of Parasitology, McGill University, Macdonald College P.O., Que., Canada. The parasites upon which this paper is based were collected by Dr. Robert E. Kuntz (CDR, MSC, USN, U. S. Naval Medical Research Unit No. 2, Taipei, Taiwan), a member of the U. S. Naval Medical Mission to East Pakistan in 1958. He was assisted by James Reese, HM, IC, USN, and Charles Knight, HCM, USN, also of NAMRU-2. Mr. H. G. Deignan, Associate Curator, Division of Birds, U. S. National Museum, identified the birds.
[2]National Research Council of Canada Postdoctorate Fellow.

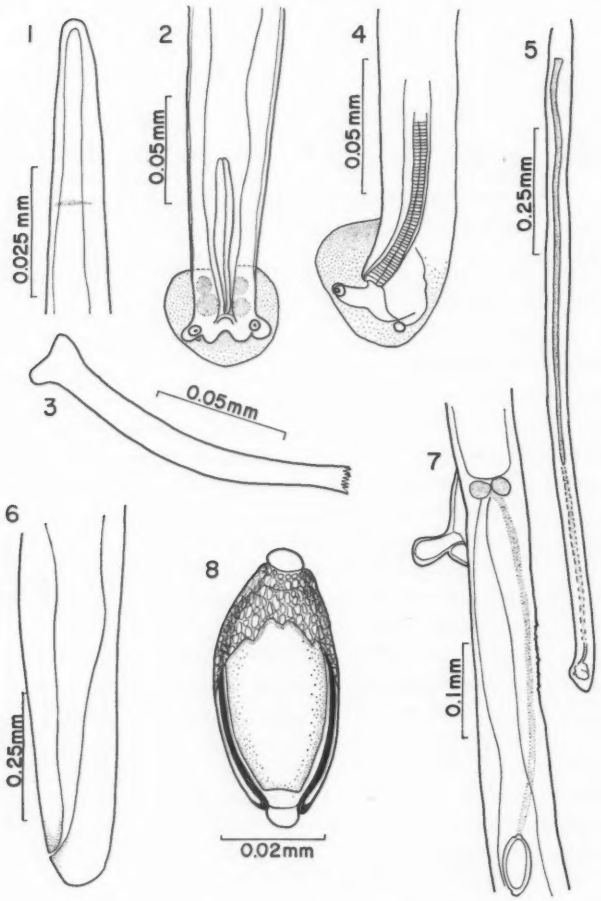

FIG. 1. Anterior portion of female, lateral view.
FIG. 2. Posterior end of male, ventral view.
FIG. 3. Spicule.
FIGS. 4 and 5. Posterior end of male, lateral view.
FIG. 6. Posterior end of female, lateral view.
FIG. 7. Region of vulva, lateral view.
FIG. 8. Egg.

Discussion

Capillaria has not been recorded previously from *Copyschus c. saularis.*

Capillaria copyschi sp. nov. resembles the following avian forms in the possession of a vulvar appendage in the females:

C. picorum Rudolphi, 1819 (3, 4, 6),

C. ovopunctata Travassos, 1915 (7),

C. caudinflata (Molin, 1858) Travassos, 1915 (7),

C. appendiculata Freitas, 1933 (6),
C. spiculata Freitas, 1933 (6),
C. bursata Freitas and Almeida, 1934 (2),
C. rudolphi Freitas, 1934 (1),
C. montevidensis Calzada, 1937 (3, 7),
C. mergi Madsen, 1945 (4),
C. quiscali Read, 1949 (5).

C. copyschi differs from *C. quiscali*, *C. caudinflata*, and *C. bursata* in the absence of lateral caudal alae, and also from *C. caudinflata* in having the spicule sheath smooth instead of spiny. *C. copyschi* differs from *C. quiscali* in not having the papillae of the bursa in the male divided into blunt dorsal and ventral rami and from *C. bursata* in that the bursa is not supported by two dorsal and ventral lobes.

C. copyschi can be distinguished from *C. picorum*, *C. rudolphi*, and *C. spiculata* in being smaller, from *C. picorum* in the absence of long ridges on the egg shell and in the possession of an untwisted spicule, from *C. rudolphi* and *C. spiculata* in the possession of a smaller and, in the latter species, untwisted spicule, from *C. rudolphi* in the absence of postanal papillae in the female, from *C. mergi* in having a reticulate rather than a granular egg shell, and from *C. ovopunctata* in the absence of punctations on the egg shell, and from *C. montevidensis* in the absence of a round papilla on each lip of the vulva and in the ratio between the anterior and posterior parts of the body. In *C. copyschi* the ratio is approximately 1:1 whereas in *C. montevidensis* it is 1:3.

C. copyschi closely resembles *C. appendiculata* in having a vulvar appendage but differs from the latter in the absence of a double membranous extension of the vulvar appendage, whereas *C. copyschi* has a cuticular inflation along the body wall anterior and posterior to the vulva. *C. copyschi* is also smaller and the tail of the male lacks large alae.

C. dujardini (= *C. columbae* sensu Baylis, 1939) (4) has been reported from birds in India but this is a form in which a cuticular vulvar appendage, as found in *C. copyschi*, is absent.

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THE INTRAOVULAR DEVELOPMENT OF THE SUBSPIRACULAR GLANDS IN HYALOPHORA CECROPIA (L.) (LEPIDOPTERA; SATURNIDAE)[1]

R. HARMSEN[2] AND W. E. BECKEL

Abstract

The subspiracular glands as found in Lepidoptera are the subject for this investigation.

The embryonic origin from the ectoderm is described.

Details of the cytology and morphological development of these glands in the egg are reported. Before hatching of the eggs, the glands undergo a nuclear secretion. The number of cells in each gland remains constant throughout the intraovular period.

The development of the glands is related to the development of other tissues.

Introduction

The term "subspiracular gland" was coined by Verson and Bisson (17). It was applied to clusters of large cells, apparently glandular, lying ventral to the spiracles and closely attached to the ventral tracheal trunks in the first eight abdominal segments of the commercial silkworm (*Bombyx mori* L.). Homologous cells have been described in other insects (1, 12, 14, 18), and named variously; the most common name is oenocytes. However, the term oenocytes has also been applied to subepidermal cells as found in *Rhodnius prolixus* Stal. (19), to subepidermal and subspiracular cells in *Tenebrio molitor* L. (21), to segmentally arranged clusters of cells in *Calliphora erythrocephala* Mg. (23), to separate cells spread through the fat body as seen in the honey bee (*Apis mellifera* L.) (7), and to glandular structures of postembryonic origin in various insect orders (15). Whether these cells are homologous to the subspiracular gland cells of Lepidoptera is a question.

Like many other endocrine glands in insects, the subspiracular glands of the Lepidoptera are ectodermal in origin, (4, 10, 12, 13, 14, 16, 17). These authors describe a differentiation of the ectoderm ventral to the spiracular invaginations, which gives rise to a cluster of large cells later found as the subspiracular glands closely adhering to the ventral tracheal trunks which extend from each tracheal manifold in the abdomen. A similar situation is described for Coleoptera and Orthoptera (4, 5, 6, 11, 18).

The subepidermal oenocytes as described for *Rhodnius* and *Periplaneta* are also of ectodermal origin (8, 19). However, these cells are spread throughout the body wall and remain part of it.

[1]Manuscript received April 26, 1960.
Contribution from the Department of Zoology, University of Toronto, Toronto, Ontario.
[2]Address after September 1, 1960, University of Cambridge, Department of Zoology, Downing Street, Cambridge, England.

In *Rhodnius* they are not only produced during embryonic development, but are created anew from undifferentiated epidermis at each ecdysis, (19, 20, 22). The subspiracular glands on the other hand are reportedly produced only during embryonic development.

For the subspiracular glands no function is known and very little is known about their morphology and cytology (1, 13, 17). The present investigation was undertaken to obtain a description of the origin and intraovular development of the subspiracular glands of Lepidoptera and to correlate their development with the development of those tissues in the body with which they may be in functional relation.

Materials and Methods

Pupae of *Hyalophora cecropia* (L.) were chilled for at least 3 months at 5° C, then placed at room temperature and moistened daily until the adults emerged. Mating pairs, as they appeared, were isolated. The eggs laid were removed every 6 hours and were kept at constant temperature and humidity. At regular intervals some eggs from each 6-hour batch were killed and fixed.

This procedure gave a series of developmental stages from no development to complete development just prior to eclosion. Approximately 20 eggs of each 6-hour batch were kept until eclosion as a control group. Instead of noting the various developmental stages as killed and fixed after a certain time of development, they were noted as killed and fixed at a certain percentage of the time required by the control group to reach complete (100%) development. In short, all stages were expressed as a percentage of complete development. This type of notation provided a simple and accurate means of comparison among eggs from various females developing at different temperatures and humidities. It also made possible comparison among eggs from different females kept at the same temperature and humidity where, for example, an egg 16 hours old from one female might be 10% different in development from an egg 16 hours old from another female.

The eggs have a hard and relatively impermeable chorion and thus fixation and sectioning of whole eggs proved to be difficult with normal techniques. However, the eggs are very large (up to 2 mm in diameter) and it was possible to slice off a small cap of the chorion with a razor blade, leaving a hole approximately .5 mm in diameter. This made fixation easy in any fixative. Alcoholic Bouin's, Zenker's, saturated sublimate, neutral formol, and Carnoy's were used.

After fixation, the eggs were embedded in paraffin (m.p. 60–63° C). After hardening, the paraffin around the chorion was broken or scraped away and the chorion was then peeled from the wax-impregnated remaining portion of the egg without doing any damage to the embryo. The embryo, still encased in yolk and vitelline membrane, was subsequently re-embedded in paraffin, and could be sectioned with ease. Sections were made in several planes at 5 μ and 10 μ thickness. The 10-μ sections, owing to the size of the gland cells, proved to be the best. All sections were stained with Hansen's trioxy haematin (an

iron haematoxylin). Sections were obtained of the following developmental stages: 23, 29, 35, 41, 44, 47, 52, 53, 59, 60, 68, 76, 84, 92, and 100% development.

The Origin of the Glands

In the 23% stage of development the germ band is developed to the point where the ectoderm starts to differentiate as the central nervous system, and the spiracular invaginations appear (Figs. 1 and 3). All along the length of the body a band of mesoderm is formed showing segmental coelomic cavities (Fig. 3). Both cephalically and caudally the enteron is being formed.

The tissue around the spiracular invaginations is homogeneous; there is no differentiation of the gland cells (Fig. 3). Many mitotic figures are in evidence. Cell membranes are obscure, giving the tissue an appearance of many nuclei suspended in a dense granular mass of cytoplasm.

In the 29% stage the embryo has developed considerably. The tracheal invaginations have branched and united to form the longitudinal tracheal trunks (Figs. 2 and 4). In the ectodermal tissue, just ventral and caudal to the spiracular invaginations, a cluster of nuclei can be observed on either side of each of the first eight abdominal segments (Figs. 4 and 8). A few mitotic

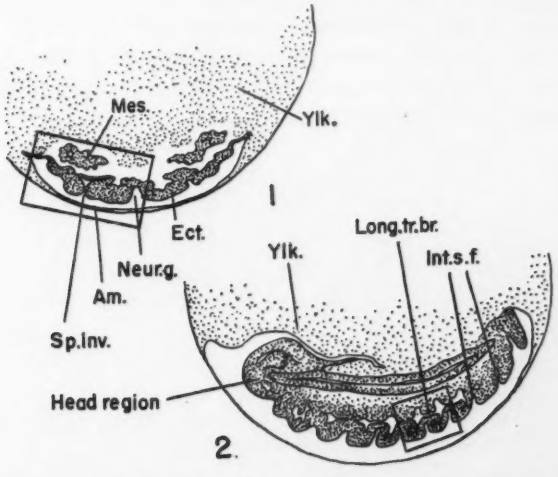


FIG. 1. Cross section through an approximately 25% developed embryo. The part included in the rectangle is shown in detail in Fig. 3.

FIG. 2. Paramedial, longitudinal section through an approximately 30% developed embryo. The part included in the rectangle is shown in detail in Fig. 4.

ABBREVIATIONS USED IN FIGS. 1–6:

Am. Amnion
Ect. Ectoderm
Ep. Epidermis
Int. s. f. Intersegmental fold
Long. tr. br. Longitudinal tracheal branch
Mes. Mesoderm
Neur. Neuroblasts
Neur. g. Neural groove
Sp. inv. Spiracular invagination
S.S.G. Subspiracular gland
Trach. inv. Tracheal invagination
Ventr. tr. Ventral tracheal branch
Ylk. Yolk

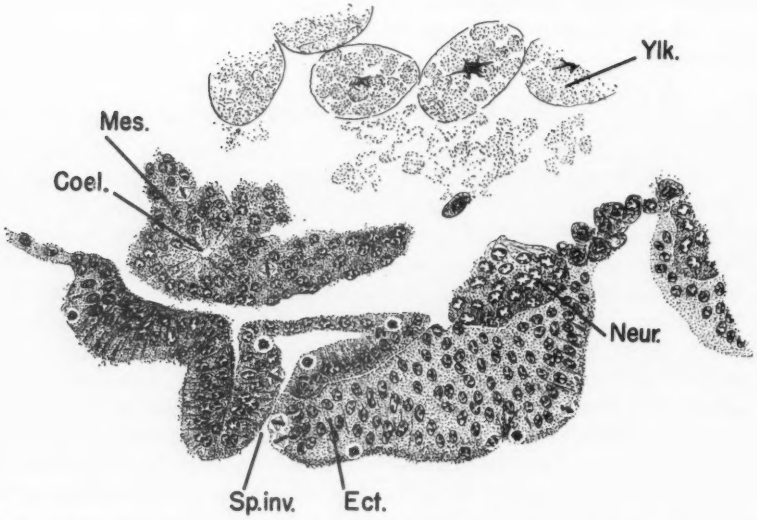


FIG. 3. Cross section through left half of germ band of future fourth abdominal segment at the 23% level of development (see Fig. 1). The ectoderm ventral to the spiracular invagination is still undifferentiated. (400× enlarged)

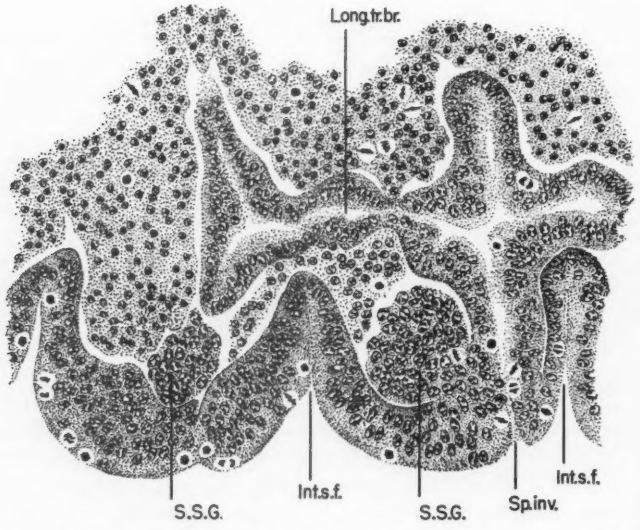


FIG. 4. Paramedial, longitudinal section through germ band of second and third abdominal segments at the 29% level of development (see Fig. 2). The subspiracular glands are differentiated from the ectoderm, caudal and ventral to the tracheal invaginations. (500×)

figures are observed among these cells (Fig. 9). The interphase nuclei are round or oval, containing a coarsely granular nucleoplasm and surrounded by a distinct nuclear membrane (Fig. 9). Their diameter varies from 3.5 μ to 6 μ, with an average diameter of approximately 5 μ.

The cytoplasm surrounding the nuclei is dense; it stains darkly and evenly, giving at most a cloudy effect. No distinct cell membranes are apparent, separating the nuclei. The shortest distance between the nuclei varied from 1 μ to 5 μ. The number of nuclei per cluster is relatively constant, and is approximately 125.

In the embryo, developed to the 35% stage, the ectodermal tissue which will become the subspiracular gland is recognizably differentiated. It is formed into a dense cluster of closely packed cells. The part of the cluster ventral to the spiracular opening is separate from other tissues. The part caudal to the spiracular opening is still attached to both the tissue of the tracheal invagination, and that part of the undifferentiated ectodermal tissue where the tubercle blast cells are to be formed (Fig. 5). Cell membranes are now present, though only faintly discernible. The cells are among the largest in the body, they are only exceeded in size by some of the tubercle blast cells. The cells are angularly oval, measuring 5 to 7.5 μ by 7.5 to 10 μ. The cytoplasm is dense and cloudy but not granular. The nuclei are oval to round, measuring 5 to 7 μ in diameter. The nucleus possesses a distinct membrane, surrounding a homogeneous nucleoplasm with coarse, loosely scattered chromatin.

The number of cells per cluster has not changed significantly since the 29% level, no further cell divisions of any kind can be observed. In all other tissues, active mitosis is still taking place.

The Period of Maturation

From the 35% level to the 60% level, the subspiracular gland cells develop slowly, without significant change. They do not increase in number and show no secretory activity. In general they maintain the same position in the body: caudal and ventral to the spiracular opening, just under and in direct contact with the epidermis and attached to the ventral tracheal trunk (Figs. 5 and 6). The cells adhere closely to one another, producing the angularly oval shape of each cell (Figs. 6 and 10). During this period the cells increase only slightly in size from an average of 6.3 by 8.8 μ at the 35% level, to an average size of 10.8 by 13.5 μ at the 60% level. The nuclei during this period remain at a fairly constant size of 5.5 by 7.0 μ.

In those tissues fixed in Bouin's, Zenker's, or sublimate the cytoplasm of the gland cells remains practically unchanged during this period, it is very dense with a cloudy opaque appearance; no granules, vacuoles, or other structures are visible (Fig. 10). In the cells fixed in Carnoy's, the cytoplasm shows an appreciable number of vacuoles (Fig. 11).

The nuclear membrane throughout this period has changed from a well-defined to an ill-defined structure surrounding a very lightly staining nucleo-

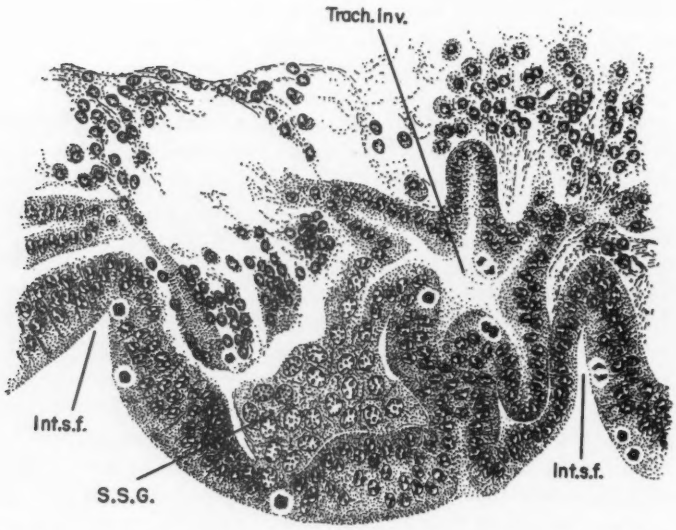


FIG. 5. Paramedial, longitudinal section through second abdominal segment at the 35% level of development. The subspiracular gland is developing into a definite tissue, still attached to epidermis and tracheal invagination. (500×)

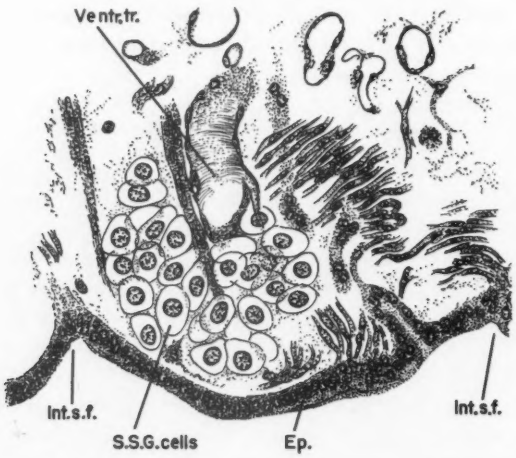


FIG. 6. Paramedial, longitudinal section through the seventh abdominal segment of the larva at the 59% level of development. The gland lies just below the epidermis, in direct contact with the ventral tracheal branch. The cells are still closely packed into a fairly tight cluster. (400×)

plasm in which is suspended a darkly staining network of threadlike and granular structures (Figs. 10 and 11). No nucleolus has been observed in any cells up to this stage.

During the greater part of the 35–55% development, the other tissues of the embryo show a rapid development with much mitotic division. This development ceases after the 55% level; all major tissues are now present in a fairly complete way. No more mitosis is observed anywhere in the embryo from this stage on.

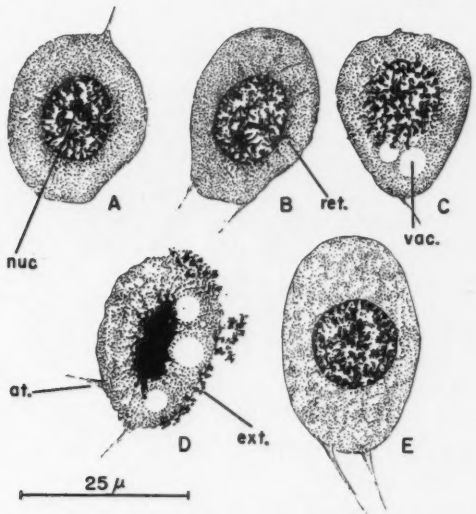


FIG. 7. The intraovular secretion cycle of a subspiracular gland cell. (A) At 84% development. (B, C, and D) Three subsequent stages at 92% development. (E) The recovered cell at 100% development.

at. attachment filament
nuc. nucleolus
vac. secretion vacuole
ret. cytoplasmic reticulum
ext. extracellular material

The Intraovular Secretion

From the 60% level of development to the moment of eclosion of the larva at the 100% level, the subspiracular glands show considerable activity. At about the 70% level, the cells, which up to that stage had adhered very closely together (Fig. 12), spread apart (Fig. 13). Consequently the gland tissue becomes very loose, the cell shape becomes more rounded, and it can be observed that the cells are attached to one another and to the surrounding tissues by a thin, filamentous material (Fig. 13).

From the 80% level on, the glands have a position which they will retain all through the larval development and in the pupa (2). They lie ventral to the spiracles between the body wall and the outermost musculature. They are closely attached to the ventral tracheal trunk. From the irregularly rounded posterior portion of the gland an extension of spindle-shaped cells runs ventrad and anteriad toward the anterior connection of the ventral scolopophorous organ to the body wall (Fig. 13). During the intraovular period of development the glands are not innervated or intracheated.

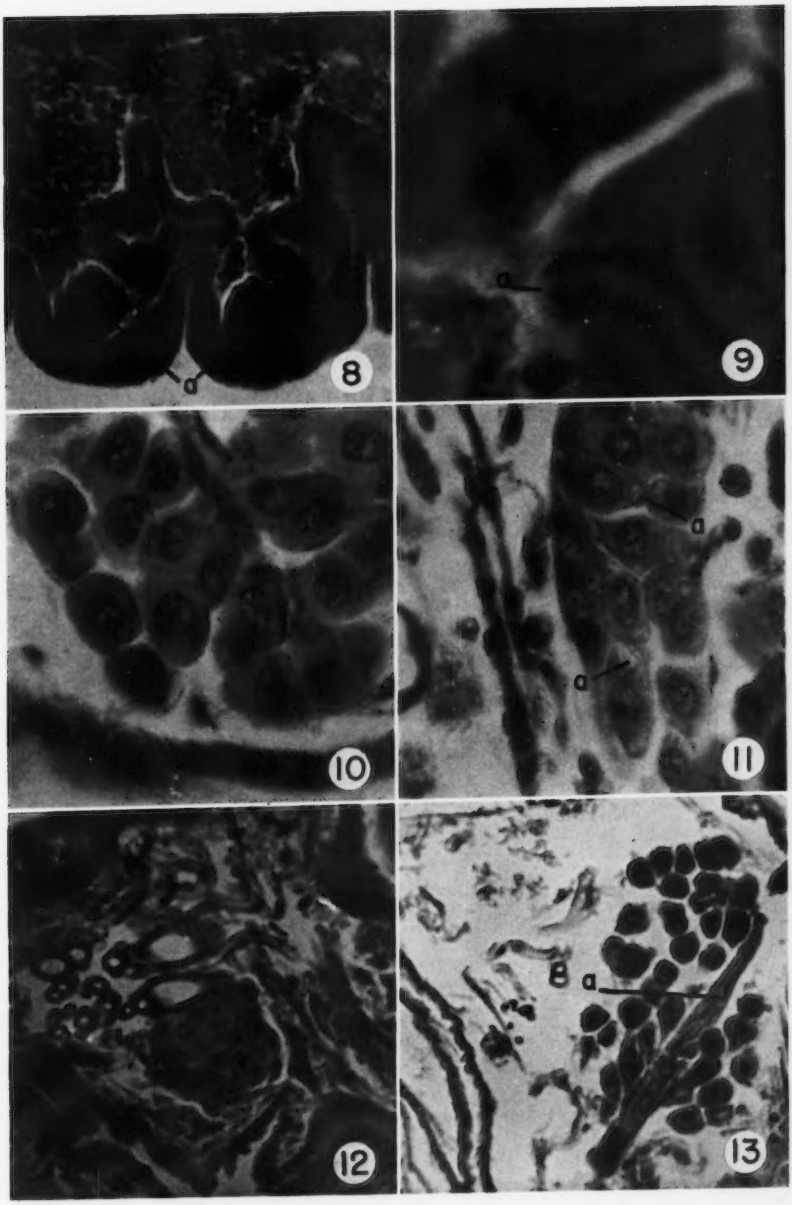
Shortly after the 90% level of development the gland cells secrete a colorless product into the blood. Up to the moment of secretion the cytoplasm remains homogeneous and dense with no inclusions. At the time of the 76% level of development, there is some evidence of a vague reticulum radiating from the nucleus. Also, from this stage on, a layer of slightly darker cytoplasm is seen around the nucleus (Figs. 7 and 14). The cells only slowly increase in size up to an average of 14 by 22 μ at the 90% level.

The nuclei during the period from 60 to 90% development increase in size rapidly from an average 5.5 by 7.0 μ to an average 10 by 12 μ. They remain round to oval. The nuclear membrane is becoming more and more indefinite, yet a sharp boundary between nucleus and cytoplasm is maintained (Fig. 7A and 7B). Definite nucleoli are present in most cells, the nucleoplasm is heterogeneous, a mesh work of coarse, irregularly shaped, darkly stained inclusions suspended in a much lighter nongranular medium. In the later stages, just before secretion, many nuclei, especially in tissue fixed in Carnoy's, show excessive shrinkage (Fig. 14).

At the 92% level of development cells can be observed with homogenous cytoplasm and the nucleus round or oval and some evidence of a nuclear membrane (Figs. 7B and 15), lying next to cells with the nucleus having an irregularly branched appearance, without any distinct boundary between it and the cytoplasm (Figs. 7C and 16). The cytoplasm of the latter cells contains many vacuoles, granules, and droplets and has a definite reticular network running through it (Fig. 7C). The cell membrane is wrinkled, showing irregular protrusions. Still other cells show the nuclei very dark and dense, and shrunk to an average size of only 4.6 by 8.6 μ, irregular in shape, with extensions into the cytoplasm (Figs. 7D and 17). The cytoplasm in these cells shows many inclusions and the cell membrane appears ruptured (Figs. 7D and 17). A finely granular, noncellular material is evident in the fixed body fluid, outside some gland cells (Figs. 7D and 18).

After this extensive secretion the cells recover quickly. At the moment of emergence the cells are back to their normal shape, round, oval, or spindle-shaped (Figs. 7E and 19). The cytoplasm is then dense and finely granular, giving a mottled or marbled appearance. Some evidence of a cytoplasmic reticulum may be observed around the nucleus. The nucleus is round or oval, with a distinct nuclear membrane enclosing coarsely granular nucleoplasm, with a concentration of particles along the nuclear membrane. There is now no nucleolus, the cells are larger, measuring an average 18 by 26 μ. The nuclei also have rapidly increased in size, now measuring an average 10 by 12 μ again.

FIG. 8. Third and fourth abdominal segment, 29% development. (*a*) Subspiracular gland.
FIG. 9. Subspiracular gland tissue, 29%. (*a*) Mitotic division figure.
FIG. 10. Subspiracular gland tissue, 59%, Bouin's fixation.
FIG. 11. Subspiracular gland tissue, 59%, Carnoy's fixation. (*a*) Vacuoles.
FIG. 12. Subspiracular gland tissue, 68%.
FIG. 13. Subspiracular gland tissue, 84%. (*a*) Ventral scolopophorous organ.



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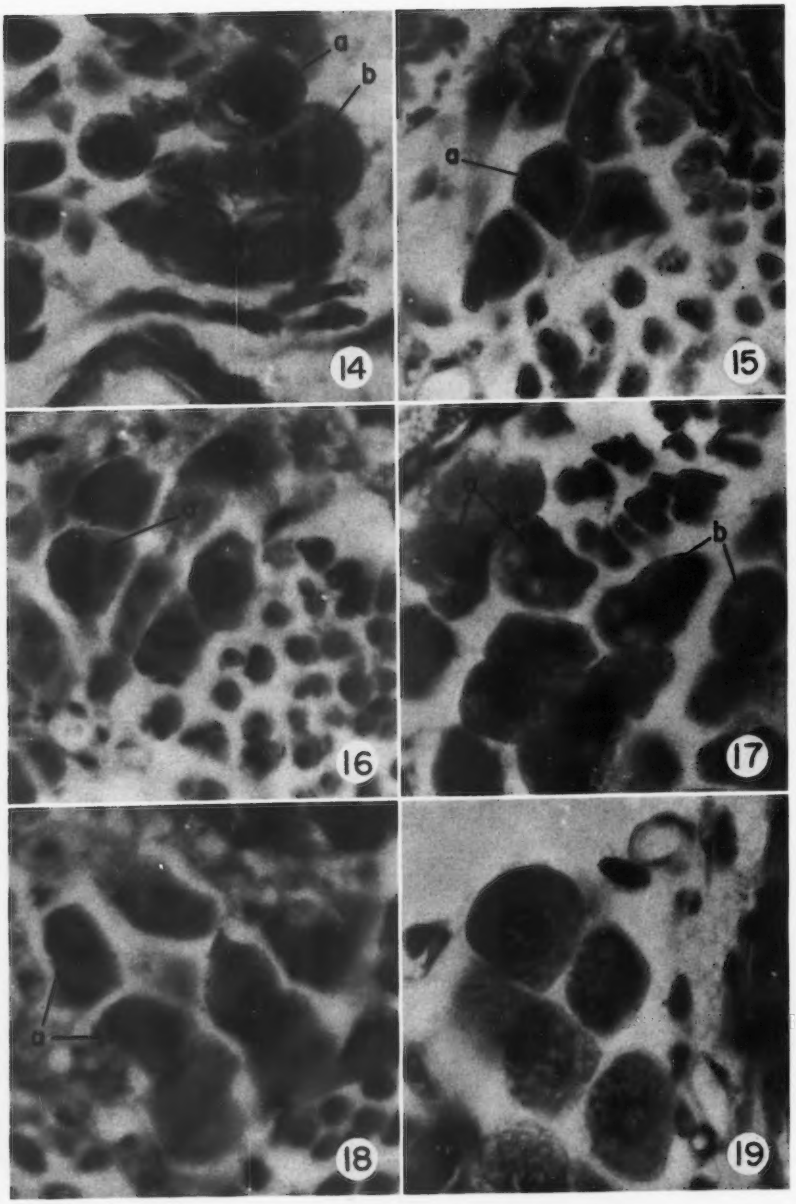

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Development of the Integument and the Fat Body

The development of these structures was observed in particular, as the literature suggests that they may be influenced by the subspiracular glands (1, 19).

At the 60% level of development the epidermis is discontinuous. It consists of dense masses of cells covering the major part of the body. At this stage of development the first sign of cuticular deposition appears in the peritreme of the spiracles. At the 68% level of development cuticular material is present on the crotchets, jaws, and peritremes. Also a thin layer, less than 1 μ of cuticular material, is seen in some places on the general epidermis and in some main tracheal branches. At the 76% level of development the epidermis has spread out and now forms a continuous thin sheet of very small cells with relatively large nuclei. The cuticle is now continuous, composed of a granular material. The cuticle of the jaws, setae, crotchets, head capsule, and peritremes is much thicker and slightly pigmented. This condition of epidermis and cuticle is still observed at the 84% level of development. By the 92% level, the time of secretion of the subspiracular glands, the epidermis has thickened considerably in some places and the cuticle appears as a thicker, 2–3 μ, continuous layer. It is pigmented a brown color throughout; only the outer surface is granular. The same situation is found at the 100% level. Within a few hours after hatching the cuticle turns black.

The first evidence of a fat body is observed in the 76% level of development, the cells are few and small, but already contain some typical fat vacuoles and droplets. The fat body cells increase in number and size until the 90% level of development, after which they slightly decrease in size, and lose most of their vacuoles. The yolk decreases in amount throughout the intraovular development and seems to be completely absorbed shortly before the 90% level of development.

Discussion and Conclusions

The ectodermal origin of the subspiracular glands is confirmed by the events observed during the 20–30% level of development in the embryo of *Hyalophora cecropia*. The glands are first observed as a discrete tissue at the 29% level of development. The cells are formed by mitotic division. After the 29% level of development no more mitotic division is observed in these gland cells. This developmental history is similar to that observed in *Bombyx mori*, (14, 17). In *Ephestia kühniella* on the contrary only one gland cell is produced mitotically. This cell later gives rise to the entire subspiracular gland by means of amitotic cell division (13).

FIG. 14. Subspiracular gland cells, 84%. (*a*) Shrinkage fixation artefact. (*b*) Denser cytoplasm around nucleus.

FIG. 15. Subspiracular gland cells, 92%. (*a*) Cell before secretion.

FIG. 16. Subspiracular gland cells, 92%. (*a*) Beginning of secretion, an irregular nuclear membrane.

FIG. 17. Subspiracular gland cells, 92%. (*a*) Contracted nuclei. (*b*) Secretion vacuoles.

FIG. 18. Subspiracular gland cells, 92%. (*a*) Extracellular material.

FIG. 19. Subspiracular gland cells, 100%. (Mottled cytoplasm.)

The formation of the gland into an entire organ is complete by the 84% level of development, including such changes as the breaking of contact with the epidermis, the spreading of the cells, the formation of attachment filaments, and the adherence of the glands to the main ventral trachea. This maturation makes possible the intraovular functioning of the glands at the 92% level of development. Such an intraovular secretion of these glands has also been reported for *Ephestia* by Stendell (13) and suggested for the subepidermal oenocytes of *Rhodnius* by Mellanby (9). The secretion of the subspiracular gland cells is a nuclear secretion, as is concluded from the variety of nuclear events observed in the secretion cycle at the 92% level of development. This nuclear secretion places the subspiracular gland, with a few other insect glands (3) in a unique place among glandular tissues. Without a detailed histochemical study of the active cells it is difficult to say what the cytoplasm contributes to the secretion. The appearance of a nucleolus in each cell shortly before the secretion cycle may be of importance. The nucleolus is no longer visible after the wave of secretion has passed.

The subspiracular glands are formed simultaneously with the nerve cord and the tracheal invaginations, but there is no evidence of any functional relation with these latter tissues. No innervation or intracheation of the gland cells has been observed in the egg. The location of the gland in close contact with the tracheal system appears to be fortuitous.

A metabolic relation between oenocytes and fat body cells has been suggested (1). The present investigation shows that concomitant with the subspiracular gland secretion at the 90–95% level of development the fat body cells begin to shrink while losing most of their vacuoles. This observation could be considered an indication of a functional relation between the two tissues. It is, however, possible that the fat body merely takes over the role of supplying food to the developing tissues at a time when the yolk is almost completely absorbed.

Whereas the function of the subspiracular oenocytes is largely unknown, the role of the subepidermal oenocytes has been clearly shown to be involved in the formation of lipid constituents of the cuticle (8, 19, 20, 21, 22). In the developing embryo of *Hyalophora cecropia* there are no subepidermal oenocytes visible. Whether the subspiracular glands are involved in lipid deposition is a question which cannot be decided on the basis of the present evidence of cuticle formation within the egg. At the moment of secretion of the subspiracular glands the cuticle completely covers the animal, and has reached its normal first instar thickness. Whether or not it has its lipid constituents is unknown. In normal larval cuticle formation the cuticulin which contains lipid, is thought to be laid down as the cuticle is formed (19, 20, 21, 22). If this is so in the first stage of the cecropia larva, then the oenocyte secretion (which is observed after the cuticle is formed) does not contribute to this lipid constituent. The wax layer, however, is normally produced at the end of cuticle formation (8, 22). Perhaps, the subspiracular glands are involved in this wax production.

From the present investigation, it can only be concluded that in Lepidoptera as represented by *Hyalophora cecropia*, a series of organs known as subspiracular glands or clusters of subspiracular oenocytes are to be found. They originate early in the intraovular period of development from the ectoderm, ventral to the spiracular invaginations in the first eight segments of the abdomen. By the time of 80% development, the glands are fully mature and each cell secretes a clear substance from the nucleus through the cytoplasm into the blood shortly before the moment of emergence. The function of these glands is as yet unknown. Their secretion takes place simultaneously, suggesting some central control or trigger mechanism but the agent of co-ordination has not as yet been discovered.

The problem of the homology or analogy of the subspiracular oenocytes with abdominal endocrine glands described for other insect orders has not been solved.

Acknowledgment

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A HISTOPATHOLOGICAL STUDY OF THE INTESTINAL LESIONS INDUCED BY ECHINORHYNCHUS LAGENIFORMIS (ACANTHOCEPHALA—ECHINORHYNCHIDAE) IN THE STARRY FLOUNDER[1]

A. PRAKASH AND JAMES R. ADAMS

Abstract

Echinorhynchus lageniformis Ekbaum, 1938, a common acanthocephalan parasite of the starry flounder, causes extensive damage to the intestinal wall of the host. The female parasite appears to penetrate more deeply than the male and induces formation of a chronic nodular outgrowth outside the intestinal wall. A histopathological study of the early and advanced lesions is reported.

Introduction

Echinorhynchus lageniformis, a new species of acanthocephalan parasite, was described by Ekbaum (1) from the starry flounder, *Platichthys stellatus* (Pallas), and the two-lined flounder, *Lepidopsetta bilineata* (Ayres). She noted that the anterior part of the body of the female worm is deeply buried in the host's intestinal wall with only the globular hind end protruding into the intestinal lumen. She further commented that the intestinal wall is frequently completely pierced by the proboscis and anterior portion of the parasite.

We wish to report in more detail the effect of this parasite on the intestinal wall as revealed by histopathological observations of the infected tissue.

Methods

The flounders were caught in Coal Harbour at Vancouver, B.C., on October 24, 1957. The intestine was removed from freshly killed animals, cut into small pieces, and fixed in Bouin's fluid. Paraffin sections were cut at 10 μ and stained with Ehrlich's or Heidenhain's iron haematoxylin and eosin for general histological examination. To obtain contrast between muscle fibers and collagen, a few sections were stained with Weigert's haematoxylin and Van Geison's picro-acid-fuchsin.

Results and Conclusions

Ekbaum (1) reported the prevalence of *Echinorhynchus lageniformis* in the starry flounder caught off Departure Bay, Vancouver Island, as high as 27%. Our observations show an equally high prevalence in fish caught in two localities near Vancouver. The proximal loop of the intestine was found to be the most frequently parasitized portion of the gut.

[1]Manuscript received June 27, 1960.
Contribution from the Department of Zoology, University of British Columbia, Vancouver, B.C.

Figures 1 and 2 show the over-all relation of the parasite to the intestinal wall. The proboscis of most individuals is embedded in the submucosa, though some extend as far as the muscularis externa. Male and female parasites seem to attach in the intestinal wall in close proximity to one another, the latter usually more deeply embedded than the former. This difference in the degree of penetration between males and females has been reported by Ekbaum and can be interpreted as an adaptation for greater mobility of the male parasite for the purpose of copulation with the females.

The intestinal mucosa at the site of penetration of the parasite shows a complete denudation of the columnar epithelium. The tissue changes around the head of the parasite are at first degenerative and later necrobiotic with cells showing pyknotic nuclei. The granulation tissue at the site of the lesions consists of small round cells (lymphocytes) and mononuclear histiocytes. An abundance of fibroblasts is also noticeable which in the immediate vicinity of the parasite tend to form a collagenic capsule (Fig. 3).

Depending on the extent of penetration by the parasite, the granulation tissue is visible either as a dark-staining mass extending from the mucosal layer to the submucosa (Fig. 3) or continuing through the muscularis externa and serosa to form a polypoid protrusion outside the intestinal wall (Fig. 2). A critical examination of this polypoid formation reveals that it is not a neoplastic tissue but a case of chronic granuloma as evidenced by the presence of irregularly scattered small round cells, mononuclear histiocytes and fibroblasts. Many newly formed blood capillaries and thin fibrous septa interspersed between the cells are additional features of the growing mass and there is a suggestion of the formation of multinucleate giant cells at one or two places. Judging from the scarcity of neutrophils and abundance of mononuclear histiocytes, the reaction appears to be a chronic rather than an acute one.

There is little in the literature with which these findings can be compared, most writers commenting only on the gross aspects of damage to the intestinal wall. Weinberg and Romanovitch (2), however, reported a study of the effect of *Macracanthorhynchus hirudinaceus* in the intestine of the pig. They described two conditions, one attributed to mechanical pressure and irritation alone, the other to the added presence of pathogenic bacteria introduced by the worm. In the former case there is no inflammation; the latter is characterized by a zone of necrotic tissue around the proboscis of the parasite. This in turn is surrounded by a zone of inflammatory infiltration consisting of mononuclear cells. In both types of lesions, eosinophils were common. The lesions observed in the present study are conspicuously deficient in eosinophils and even in advanced necrosis, no bacteria were observed. As most of the damage to the intestinal wall and subsequent formation of the polypoid protrusions outside is associated largely with female parasites, it can be concluded that in the present case the severity of the infection is largely a matter of the degree of penetration by the parasite and not necessarily due to the introduction of pathogenic bacteria.

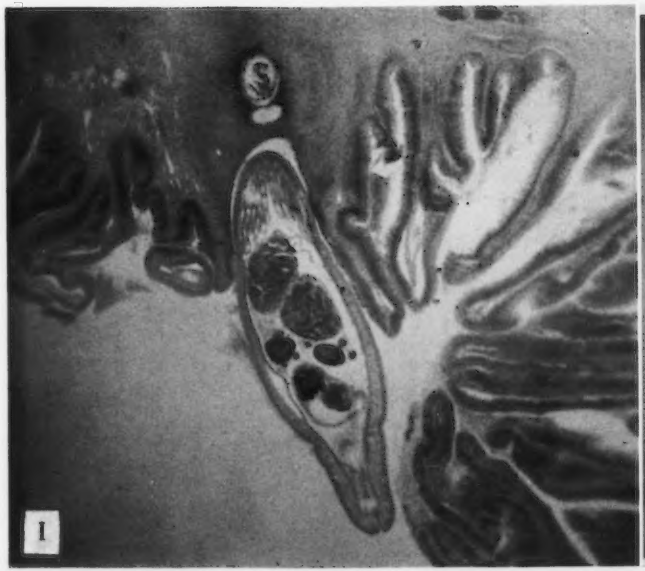

FIG. 1. Section of the intestinal wall showing male worm attached to the mucosal layer.

FIG. 2. Section of the intestinal wall showing deep penetration by female worm, extensive tissue damage, and polypoid formation.

PLATE II

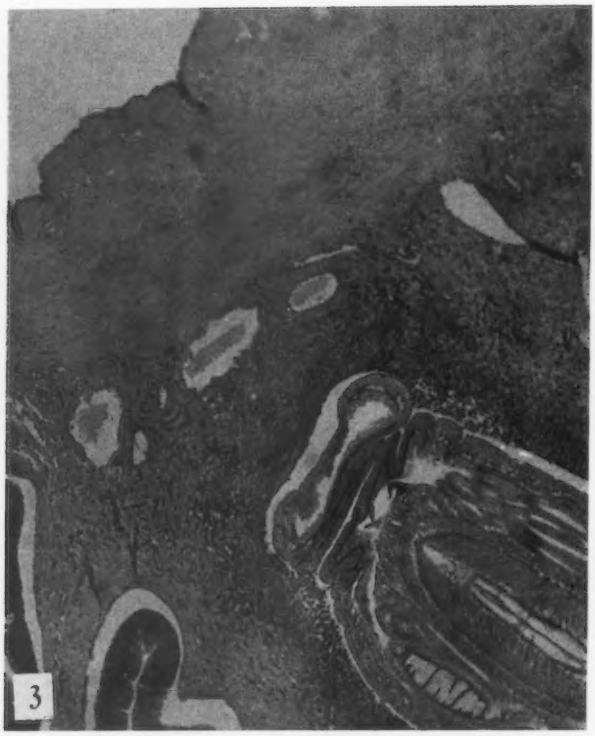

FIG. 3. The granulation tissue and collagenic capsule around the head of the parasite in the submucosa.

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EFFECTS OF ARTIFICIALLY PRODUCED ATMOSPHERIC ELECTRICAL FIELDS UPON THE ACTIVITY OF SOME ADULT DIPTERA[1]

D. K. EDWARDS[2]

Abstract

This paper describes some effects of experimental electrical fields on the amount of movement of *Drosophila* and *Calliphora*. Activity in *Drosophila* was temporarily reduced by sudden exposure to a potential gradient as low as 10 to 62.5 v/cm and of constant polarity. The period of reduced activity was prolonged by reversing the field polarity at 5-minute intervals. A more transient reduction of activity was observed in *Calliphora*; however, a much stronger field was necessary to produce the effect. The results do not support the idea that prestorm increases in insect activity are related to potential gradient disturbances. The possibility of effects of insect size on the response to an electrical field is discussed.

Introduction

There are occasional suggestions in the literature that changes in the behavior of some insects immediately before certain storms may be related to accompanying changes in the electrical condition of the atmosphere (4, 18, 20). Fabre (4) in his observations on the behavior of the dung-beetle *Geotrupes* states (p. 287), "They seem to be influenced above all by the electric tension of the atmosphere. On hot and sultry evenings, when a storm is brewing, I see them moving about even more than usual. The morrow is always marked by violent claps of thunder." In his discussion, Fabre did not distinguish between the possible effects of atmospheric electrical and pressure changes. Increased activity in various biting Diptera has often been observed prior to certain storms. This has been discussed from the point of view of barometric pressure effects by Wellington (19).

When possible biological effects are considered two principal aspects of atmospheric electricity must be distinguished. These are: (*a*) the potential gradient or electrical field, and (*b*) the density of unipolar air ions. The term "electrical field" here refers to the lines of force joining opposite electrical charges on the surface of the earth and in the upper atmosphere. During fair weather, the positive pole is in the upper atmosphere, the earth being negative: this produces a "positive field". The term "potential gradient" refers to the change with height above the earth's surface of the field intensity, or the potential to earth.

As a result of the "electrode effect" in the earth's electrical field, there is a conduction current of positive charges downward toward the earth's surface. This current is the result of unipolar air ions in the atmosphere. Air ions are produced by a variety of factors, such as cosmic radiation and radioactive elements in the soil. These charged particles vary in size from single molecules

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to large condensation (Aitken) nuclei and have a single electrical sign. An excess number of ions of one sign over those of the opposite sign results in a "space charge"; and a space charge may exist in fairly localized "clouds" which can be carried over the ground by wind currents. Localized changes in the unipolar ion density (space charge) may be closely related, in nature, to potential gradient fluctuations (2).

In the present paper we will be concerned only with the first aspect of atmospheric electricity, namely, the electrical field. The effects of ions upon insects will be dealt with at a later date. Often dramatic changes in sign and value of the electrical field are known to be associated with certain types of frontal weather (6, 9, 10). To date, however, few attempts have been made, either in the field or laboratory, to determine whether the electrical field in the atmosphere near the earth's surface influences insect activity, particularly before and during a storm. Silvo (17), in experiments with *Tribolium* in artificial fields, did not separate field effects on mortality from temperature effects resulting from the experimental apparatus. Schuà (14) made some outdoor observations of bee activity near hives and recorded changes in the potential gradient and other variables. Foraging frequency and sucking capacity were disturbed (more variable) when there were frequent changes in the potential gradient. However, Schuà made only intermittent records of the pressure changes occurring over the fairly long period of observation. Avio and Tarozzi (1) studied *Drosophila* oviposition under the influence of a static field. No field effect on the number of eggs deposited could be found.

There are some reports of electrical field effects on mammals. Courvoisier (3) has discussed the possibility of a biological action-spectrum for field fluctuation-frequencies, suggesting that certain frequencies may produce certain, specific, biological effects. He has emphasized the need for more experimental work with artificial-field oscillations. Frey (8) reported changes in the cardiac output in humans under the influence of an artificial electrical field. Schuà (15) found that fluctuating fields could influence the location of hamster's nests in different parts of a cage. Flad-Schnorrenberg (5) kept records over a long period of time and found a relationship between urine excretion in hamsters and weather systems. She concluded that urine excretion could be related to long-wave electromagnetic radiation accompanying storms.

This report describes an attempt to establish whether insect motor activity may be influenced by experimental application of an electrical field. Motion was used as an index of activity level because the number in motion among a group of insects could be determined more or less instantaneously at regular time intervals. Thus, the experimental conditions could be imposed or removed while monitoring the level of activity of the insects in the group.

Methods

The flies used in the present experiments were adult *Drosophila melanogaster* Meig. and *Calliphora vicina* R.D. The *Drosophila* were taken from a population cultured with an agar – molasses – corn meal medium, and maintained continuously in the present laboratory for approximately one year.

The *Calliphora* adults were laboratory-reared offspring of adults collected in the field. The *Calliphora* were reared on an artificial culture medium in the incubator along with *Drosophila.*

(a) Drosophila in Constant Field; Contacting One Pole

Four adult female *D. melanogaster* of unknown age were used in each experiment. The insects were removed from the laboratory culture and put immediately into a small plastic box (7.5×3×2.5 cm) without etherization. The bottom inner surface of the box was covered with a fine brass screen connected to earth with a wire to the outside of the box. The top was covered with 30-mesh plastic screen. The box was fastened in a clamp stand with the open, screened, surface upward. A copper plate 15×12 cm was fixed horizontally directly above the box and electrically insulated from it. The plate was 4 mm from the top of the plastic box (2.5 cm above the earthed screen in the bottom). To establish an electrical field between the copper field plate and the earthed screen, a direct current source was used, the voltage of which could be varied.

The insects were free to walk up the sides of the container, and thus could come within 4 mm of the field plate. Insects this close to the field plate would be subjected to a somewhat stronger field than those at the bottom of the container, because of possible surface leakage and polarization of the plexiglass.

Counts of the number of insects moving (walking) in the container were made visually at intervals of 10 seconds throughout the control and experimental periods. No distinction was made between walking and flying movements; flight was seldom observed in the comparatively small experimental containers. A control period of 15 minutes duration was included at the beginning of each experiment, with the upper field plate earthed. At the end of the control period the lead from the field plate was removed from the earth connection and clipped to either the positive or negative terminal of the voltage supply, the opposite pole being earthed. Thus, a charge was bound on the insects in contact with the earthed pole. The experimental period was run for 15 minutes. At the end of this time the field plate was again earthed, thus releasing the charge on the insects. A second control period was then added. All experiments (11) of this type were carried out indoors in normal daylight. The potentials used on the field plate ranged from 25 to 1350 volts. The temperature of the room was 23° C, R.H. 40%. The barometric pressure was relatively constant during the experimental periods.

(b) Drosophila in Field with Reversing Polarity

The procedure outlined above for experiments with a static or constant field was followed, except that the polarity of the field was reversed at 5-minute intervals.

(c) Drosophila in Field; Not Contacting One Pole

Two experiments were carried out using the same timing procedure as in (*a*) and (*b*), but with the insects suspended in air between two metal plates of 15×12 cm. Four insects were put without etherization into a glass tube

with inside diameter of 7 mm and length 10 cm. The ends were plugged with absorbent cotton. The tube was clamped between, and insulated from direct contact with, the two horizontal plates 2.5 cm apart. The upper plate was connected to the negative terminal of the power supply; the lower plate was positive and earthed. The potential between the two plates during the experimental period was the same as the highest value in part (*a*), or 1350 v.

(d) Calliphora in Constant and Reversing Fields

Experiments with *Calliphora* were carried out using the procedures described in (*a*) and (*b*) for *Drosophila*. Four adult females were used in each experiment. However, since the *Calliphora* were slightly larger than a housefly it was necessary to use a larger, shallow, plastic box (16×7.5×2.5 cm) and hence a larger field plate (30×30 cm). The entire assembly was turned on its side, so that the experimental field was horizontal. This was done so that the insects could be observed through the largest side of the shallow box. The insects were viewed through a copper-wire earthed screen in the vertical bottom of the plastic container. The distance between the field plate and earthed screens was 3 cm, compared with 2.5 cm in the *Drosophila* apparatus.

Experiments were carried out, as with *Drosophila*, using different potentials of constant polarity. In addition, several experiments were run with the polarity being reversed at 5- and 2-minute intervals. The experimental potentials used ranged from 30 v to 1970 v. Thirty volts in this container gave the same potential gradient to the earthed screen as 25 v in the *Drosophila* container.

Results

At the end of each minute in the experiments the six values obtained by visual counting were summed. The 1-minute sum was plotted as a point representing the activity value through the preceding minute. The polarity indicated in each figure below refers to the sign of the charge on the field plate.

TABLE I

Means and standard errors for 1-minute sums of number of moving *Drosophila* in two control periods and one experimental period in 11 experiments; $n = 15$

Expt.	Voltage	Control 1	Experimental	Control 2
1	1350	14.46±0.62	8.60±1.25*	11.86±0.58*
2	300	10.60±0.55	8.26±0.51*	10.66±0.46
3	300	13.13±0.64	8.80±0.54*	9.33±0.45*
4	300	10.60±0.41	9.00±0.66	9.93±0.34
5	300	9.93±0.34	5.66±0.45*	8.60[a]
6	100	14.00±0.73	14.06±0.93	14.40±0.71
7	50	18.20±0.43	13.06±0.74*	11.20±0.68*
8	25	15.80±0.62	13.33±0.78	10.66±0.62*
9	25	10.66±0.62	11.73±0.79	13.25[a]
10	25	19.80±0.54	17.46±0.88	15.73±0.56*
11	25	18.20±0.47	12.46±0.54*	14.53±1.02*

[a] $n = 4$.
*Significantly different from control 1 at 5% level.

(a) Drosophila in Constant Field; Touching One Pole

Table I gives the means and standard errors for 1-minute sums of the number of moving *Drosophila* in two control periods and one experimental period in 11 experiments. In all but two cases, n is 15. Means in the experimental period and second control period (control 2) which differ significantly from the corresponding control 1 mean are indicated.

Comparison of 95% confidence limits showed 6 out of 11 values for the experimental period to be lower than the corresponding mean for control 1. Similarly, six out of nine control 2 means were significantly lower than the control 1 mean. These data indicate a reduction of activity in the insects during application of the experimental field and a carry-over of the effect into control 2.

It is possible to consider all the experiments collectively by applying a paired-t test comparing: (1) control 1 and experimental means; (2) control 1 and control 2 means; and (3) experimental and control 2 means. In applying the paired-t test it must be assumed that there was no significant difference in the data as a result of differences in the experimental field strength used. Examination of the data showed, with the exception of experiment 1, no apparent quantitative relationship between activity effect and strength of the field, within the range 25 to 300 v.

Paired-t analyses showed: (1) the experimental means were significantly lower than the control 1 means; (2) control 2 means were lower than control 1 means; and (3) there was no difference between experimental and control 2 means, again indicating a carry-over effect.

Examination of the curves themselves revealed a tendency toward a rapid reduction of activity during the first part of the experimental period (first few points) followed in many cases by a trend upward toward the control 1 value. A paired-t test was made comparing the mean for the first eight points (half) of the experimental period with the mean for the first control period. These means, together with the corresponding differences between control and experimental periods, are indicated in Table II. The differences were all consistent in that the experimental mean for the 1-minute sums was always lower than the control 1 mean. There was significant ($P < 0.01$) lowering of the activity during the first half of the period of experimental application of the electrical field.

A paired-t comparison between the second half of the experimental period (seven 1-minute sums) and control 1 showed no significant difference between the two, indicating a trend toward recovery of the original activity level

TABLE II

Means of 1-minute sums for control 1 (C), means of first eight 1-minute sums of experimental period (E), with differences between control 1 and experimental values (C−E), for *Drosophila*

C	14.46	10.60	13.13	10.60	9.93	14.00	18.20	15.80	10.66	19.80	18.20
E	4.87	7.37	7.87	7.75	5.87	11.62	13.25	15.25	10.12	16.25	12.25
C−E	9.59	3.23	5.26	2.85	4.06	2.38	4.95	0.55	0.54	3.55	5.95

t (difference) = 5.06; t (1%) = 3.17

while the field remained on. A similar comparison between the two halves of the experimental period showed no significant difference, indicating that the activity during the second half of the experimental period lay somewhere between that of the first half and control 1. There was considerable variation between the curves in the trend in the second part of the experimental period.

The curve obtained in experiment 1 is shown in Fig. 1(*a*). At the end of the initial 15-minute control period the field plate was made 1350 v negative with respect to the screen in the insect container. This resulted in a considerable reduction in movement of the insects for about 10 minutes. The period of

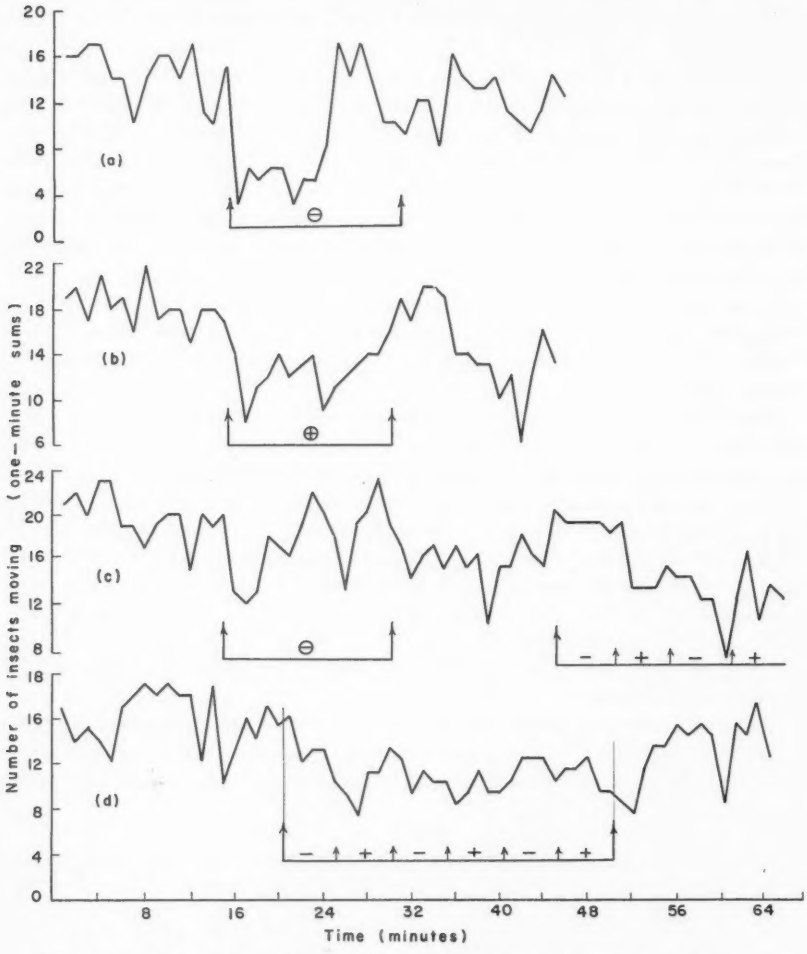

FIG. 1. Sums of number of *Drosophila* moving at different times. Periods of exposure to fields of different polarities are indicated: (*a*) 1350 v/2.5 cm; (*b*) 25 v; (*c*) 25 v steady and alternating polarity; (*d*) 25 v alternating polarity.

reduced activity was clearly followed by recovery while the field was still present. The recovered level of activity persisted through the ensuing 15-minute control period.

Figure 1(*b*) shows the curve for experiment 11. The potential on the field plate in this experiment was +25 v with respect to the earthed screen. It is apparent that the period of field application resulted in a definite reduction in activity. This effect persisted for approximately 12 minutes, at which time recovery of the original activity level was initiated. Earthing of the field plate, and subsequent elimination of the field, in the last control period was followed, but not as quickly by a second reduction in movement.

The first 15-minute period with electrical field shown in Fig. 1(*c*) is the curve for experiment 10. The potential on the field plate was 25 v with respect to earth. There is a 2–3 minute period of activity reduction immediately following exposure to the field. The initial activity reduction was followed by increased variability and a trend toward recovery of the former activity level while the field remained on. Earthing of the field plate was followed by another reduction in activity.

In the experiments with a constant field there was no indication of an effect related to the polarity of the field plate.

(b) Drosophila in Field with Reversing Polarity

The latter part of the curve in Fig. 1(*c*) shows the activity level of *Drosophila* during an experiment with alternation of the sign of polarity (25 v) at 5-minute intervals. During the period of alternation of polarity the level of activity of the insects dropped considerably.

Figure 1(*d*) represents a repeat of the experiment with alternation of the sign. Here, however, the period of alternating polarity is extended over 30 minutes and this is then followed by a control period. As in Fig. 1(*c*) the period of alternating polarity coincided with reduction of the activity level. In contrast with the activity in a constant field the reduction in activity shown in Fig. 1(*d*) was maintained fairly consistently throughout the period of field. There was no indication of a trend toward recovery of the original activity level until the field was removed.

The 1-minute sums for the experimental period in Fig. 1(*d*) may be compared statistically with those for control 1 and control 2 means. The mean level of 1-minute sums during the initial control period was *15.8*. The mean level during the experimental period was *10.9*. It is possible to place confidence limits about the respective means. Calculations based upon the individual activity values which make up the 1-minute sums showed the mean number of insects moving at each estimate, with 99% confidence limits, to be 2.63 ± 0.19 (d.f. 119) for the initial control period and 1.78 ± 0.12 (d.f. 179) for the experimental period. The reduced amount of movement among the four insects during the experimental (alternating polarity) period was significant at the 1% level. Further, the mean for the second control period may be compared with that for the experimental period. The second control mean, with 95%

confidence limits, was 2.095 ± 0.16. This mean was significantly higher (at 5% but not at 1%) than that of the experimental period, but was still lower than that for the first control period.

(c) Drosophila in Field; Not Contacting One Pole

Figure 2 shows the curve for level of activity of four *Drosophila* suspended in a container between two field plates and insulated from them. The initial and final 15-minute periods are controls. During the 15-minute experimental period the upper plate was made negative with respect to the lower plate. The potential between the plates was 1350 v.

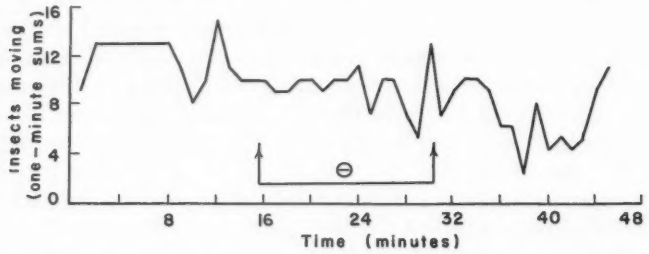

FIG. 2. Sums of number of *Drosophila* moving at different times and insulated from poles. Experimental potential 1350 v/2.5 cm.

Although the potential gradient used in this experiment was the same as that used in Fig. 1(*a*), there was little suggestion of an effect of the field upon the activity level of the insects. The contrast with Fig. 1(*a*) is particularly striking during the first half of the period of field application.

(d) Calliphora in Constant and Reversing Fields

Several experiments with *Calliphora* females were carried out using a potential of 30 v to the earthed screen in the container, and an alternating field with period 5 and 2 minutes. In no case was there a clear response to the electrical field, even when the latter had been applied for over 1 hour. The potential gradient was the same as that in the 25-v *Drosophila* experiments.

In constant-field experiments, there was no activity response in one experiment with a potential of 30 v. Figure 3(*a*) shows the activity curve obtained in an experiment with 300 v. There was no clear activity response during the period of electrical field, although there was a suggestion of a slight, transitional, depression of activity immediately following initial application of the field. In an experiment using 1350 v there was a very small and transitory reduction in activity following application of the field.

Six experiments were carried out using a constant field of 1970 v. The means and standard errors for 1-minute sums of the numbers of moving insects in two control periods and one experimental period are given in Table III. Values which are significantly different from the corresponding control 1 mean are indicated.

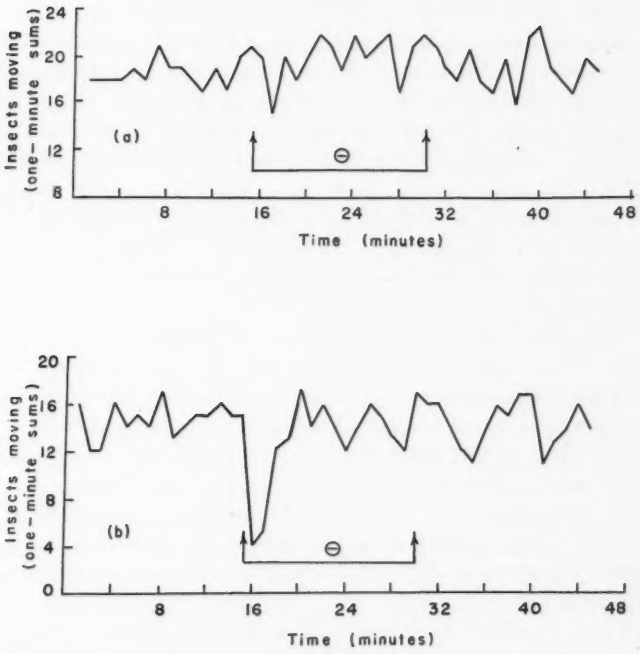

FIG. 3. Sums of number of *Calliphora* moving at different times, with experimental potentials: (*a*) 300 v/3 cm; (*b*) 1970 v.

TABLE III

Means and standard errors for 1-minute sums of number of moving *Calliphora* in two control periods and one experimental period; electrical field 657 v/cm; $n = 15$

Expt.	Control 1	Experimental	Control 2
1	15.06±0.57	17.60±1.27	18.80±0.49*
2	18.33±0.67	18.80±0.59	19.53±0.85
3	15.53±0.55	13.60±0.67	15.00±0.83
4	14.20±0.47	15.86±1.32	18.00±0.83*
5	17.00±0.36	16.13±0.61	21.06±0.48*
6	14.60±0.37	12.93±0.99	14.40±0.51

*Significantly different from control 1 at 5% level.

It can be seen from the table that none of the experimental means, and only half of the control 2 means differed from the appropriate control 1 mean. A paired-*t* comparison showed no significant difference between control 1 and experimental values, considered collectively, and no difference between control 1 and control 2. However, control 2 was higher than the experimental values at the 5% level of significance. The difference between these comparatively negative results and the *Drosophila* data is especially significant in view of the fact that the field used in the *Drosophila* experiments was considerably lower than that used with *Calliphora*.

Examination of the 1970-v activity curves indicated that there was an activity response following immediately after initial application of the field (Fig. 3(*b*)). However, the activity effect was always of comparatively short duration (around 3 minutes). This effect was masked when the entire experimental period was compared statistically with the first control period. Table IV is a comparison of the first five points (total of 5 minutes duration) in the 15-minute experimental period with the mean of the corresponding control 1 period. An experimental point lower than the mean for control 1 is indicated with a negative sign. In most cases point-number-one in the experimental field period was much lower than the control mean. The number of points lower than the control 1 mean, in the six experiments, falls off with time after the end of the first minute. The first experimental point was lower than the control 1 mean in all six experiments. Five out of six point-number-two's were lower than the control mean, and one point was higher. The ratio of the number of lower to number of higher points decreases after one passes minute one. Thus, there was a definite, but short-lived initial reduction in activity following application of the experimental field. During the period of reduced activity those insects which were not walking about were usually observed vigorously rubbing together their front legs and cleaning their wings. This behavior seemed characteristic of stationary insects during the reduced-activity period.

TABLE IV

Comparison of first five points (1-minute sums) of *Calliphora* experimental periods with mean of 1-minute sums for control 1; negative sign indicates point below, positive sign point above, control mean; experimental field 1970 v

Expt.	Control 1 mean	Pt.1	Pt.2	Pt.3	Pt.4	Pt.5
1	15.06	− 6	−10	15	−14	−14
2	18.33	−15	−16	+21	18	+22
3	15.53	− 9	+17	−14	−12	−11
4	14.20	− 1	−11	−13	+16	+17
5	17.00	−12	−12	−13	+18	+18
6	14.60	− 4	− 5	−12	−13	+17
Ratio − to +		6:0	5:1	4:1	3:2	2:4

Figure 3(*b*) shows the curve obtained in experiment 6 using a potential of 1970 v. The short period of activity reduction resulting from application of the electrical field is clearly indicated. The level of activity following the period of reduction was about the same as that of control 1.

It is apparent that, although *Calliphora* responded briefly in the same way as *Drosophila* to application of an electrical field, i.e., by a reduction in amount of activity, production of the response required a much stronger field in the former. In addition, recovery of the original activity level after the initial response was more definite in *Calliphora*.

Discussion

The results of the experiments indicate that the activity of adult *Drosophila* and *Calliphora* can be influenced by some electrical field strengths. It is not definitely known how the insects actually did perceive the electrical field changes. The activity (walking) in both *Drosophila* and *Calliphora* was reduced following a change in either the polarity or the application of the field.

A stronger field was needed to affect activity significantly in *Calliphora* compared with *Drosophila*. *Calliphora* did not respond to a potential of 30 v in either alternating or static fields, whereas a similar potential affected *Drosophila*. In the latter a potential of 300 v caused a clear-cut activity reduction, but there was little, if any, response to this potential in *Calliphora*. A potential of 1350 v produced a pronounced and prolonged reaction in *Drosophila*; a similar potential caused only a slight reaction in *Calliphora*. A potential of 1970 v was necessary to produce a definite, but nevertheless short-lived, activity reduction in *Calliphora*. Thus, there is a likelihood of considerable differences existing between different species of insects in their response to electrical fields or bound charges.

That the insects responded to the *change* in electrical field (or resulting bound charge) rather than to the static field per se is indicated by two observations. First, in experiments with a field of constant polarity the initial reduction in activity upon first exposure to the field was generally followed by a trend toward recovery of the earlier activity level while the field remained. This recovery was especially marked in *Calliphora*; it was partly obscured in *Drosophila* by increased variability in the data following application of the field. Secondly, by reversing the polarity of the field at 5-minute intervals the resulting initial reduction of the activity level of *Drosophila* was maintained fairly consistently throughout the period of alternating polarity, showing no trend toward the original level until the field was removed.

Little can be said at present regarding the ways in which *Drosophila* and *Calliphora* perceived the changes in electrical field. However, some speculations might be of value. It is suggested that they were responding to an accumulation of a charge on their bodies. The charge on the field plate would hold an equal and opposite charge on the earthed screen in the box, and likewise on the box itself. Although the insects were often touching the sides of the plexiglass, a good insulator, they would still be subject to physical contact with an excess charge of one sign due to field-induced polarization of the plexiglass and to a certain amount of surface leakage. When the insects were insulated from physical contact with one pole, and hence could gain no net charge, no field effect on activity was evident. The density of the charge on the insects in contact with one pole would be increased by their being physical projections in the direction of the field plate. It has been observed many times in the present laboratory that a high charge (held by a potential of about a thousand volts per cm) on an adult *Drosophila* resting on a conductor causes the wings to be repelled from the body in the manner of the

leaves of an electroscope. Thus, it is possible that some electroscopic action of this type, involving movement of small sensory bristles or of the wings themselves, might enable the insects to perceive a charge of the small order of magnitude bound on them in the present experiments. In the experiments, no obvious electroscopic action of the wings was observed, but this does not eliminate the possibility that a small stress of this kind was experienced by the insect.

Silsbee (16) states, "If a large charge is accumulated on a small body, the tendency to repel charges of the same sign may become very considerable, whereas if the same amount of charge is spread over a larger body the repulsive force will be less". This surface effect (i.e. how much charge the body will hold with a given repulsive force) would apply to the repelling force between a movable organ and the surface of the insect. Hence, it is reasonable to expect that a greater charge would be necessary to move, or to cause stress on, a more massive surface-organ (smaller surface-area to volume ratio), such as the wings on *Calliphora*, than a less massive one (greater surface-area to volume ratio), such as the wings on *Drosophila*. Thus, the possibility of a relationship between insect size and response to a static charge exists. The important factor, however, would be the mass of the hypothetical sensory mechanism rather than the mass of the insect per se.

In attempts to relate insect activity to particular meteorological conditions it is necessary to compare the experimental conditions with those found in nature. Schonland (13) stated that when an active storm is overhead the potential gradient at the earth's surface is usually of the order of 100 v/cm, and is never higher than 500 v/cm. In Fleming (6) it is reported that when a thundercloud is within a few kilometers of the observer, the predischarge field ranges from 100 to 300 v/cm the sign of the field usually being negative (i.e. negative pole is in the atmosphere, with earth positive). Schonland (12) also reported that in storms from which little rain is falling the negative field persists while the cloud passes overhead. The electrical field below shower clouds is generally negative and may reach a value of 100 v/cm. Freier (7) gives a sample curve for the electric field near the earth's surface which he describes as "typical for some ordinary clouds passing overhead". The curve shows deflections indicating a change somewhat in excess of 21 v/cm and lasting approximately 10 minutes. Although no polarity is indicated the field change is presumably in a negative direction.

As would be the case with resting insects in nature, those in the experiments affected by the field were in physical contact with one pole. In the experiments with *Drosophila* the minimum potential used to produce an effect on activity was 25 v. This gave a potential gradient of 10 v/cm to the earthed screen in the insect container. However, since the insects were free to walk up the side of the container, thus approaching the field plate, the minimum potential gradient to which they were exposed and which produced observable effects was between 10 and 62.5 v/cm, depending upon the position of the insect. A lower potential gradient was not investigated. These relatively low potential

gradients lie within the natural limits found during some storms. They are not far from values found during the passage overhead of certain kinds of clouds. On the other hand, potential gradients which were necessary to produce any effects on *Calliphora* all lay well outside the limits reasonably expected to be found in nature.

Fairly rapid alternations in the polarity of the electrical field or potential gradient are often associated with various types of storm conditions (6, 10). The period of change in sign can be as short as 1 minute. Fuchs (9) has shown that in general there is a considerable difference between warm and cold fronts in the changes evidenced in the potential gradient curve. Cold fronts of the second order of Bergeron (strong turbulence) are usually accompanied by frequent changes in sign and strength of the field near the earth's surface. The frequency of alternation of the field polarity used in the present studies (5 minutes) is not unrealistic in relation to the frequency range which might be expected to occur in nature.

Gourdon (11) reported a situation wherein insect activity was reduced by the effects of a storm. However, his cases of persistent torpor in vine moths, which he attributed to effects of ozone, were poststorm phenomena. It is unlikely, therefore, that they resulted from potential gradient fluctuations, since these are damped considerably in the postfrontal period in comparison with periods preceding and during frontal passage.

The present results do not support suggestions that the often-noticed prestorm increases in activity in some Diptera are related to disturbances of the potential gradient. The increased activity reported in the field may be more closely related to some factor other than potential gradient, such as pressure changes or air-ion density. It must be remembered that in considering the effects of electrical fluctuations on insect activity in nature it is necessary also to take into account the influence of other, superimposed, environmental factors.

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CRICONEMA CELETUM, N. SP. (NEMATODA:CRICONEMATIDAE) FROM AFRICAN VIOLETS IN CANADA[1]

LIANG-YU WU

Abstract

Criconema celetum, n. sp., is described from African violets collected at St. Laurent, Quebec. The body has 40–43 annules, each having a row of spines except at the caudal end; those near the middle of the body each having a row of about 70 spines. The head consists of two annules with spines, the first 22–28 μ in diameter and the second 19–23.5 μ. The annules at the caudal end have spatulate projections each with several spines. The spear is 84.3–95 μ (with one exception, 100 μ) long. The body is coated with soil particles under and around the spines.

A few pots of diseased African violets were received for examination in April, 1959, from a householder at St. Laurent, Quebec, Canada. Two species of *Criconema* were found. One of these, represented by hundreds of specimens, is a new species. It is close to *Criconema multisquamatum* (Kirjanova) (2), n. comb., Chitwood (1), and to *C. fimbriatum* (Cobb) Taylor (3).

The internal organs did not stain well with cotton blue in lactophenol. In addition, a large quantity of soil particles, collected under each row of spines, interfered with observations. The internal stuctures showed more plainly when stained with alum cochineal or acid fuchsin and mounted in balsam.

Criconema celetum, new species

(Figs. 1–8)

Female.—Twenty-eight specimens examined. Length 0.412–0.511 mm; width at middle of body, not including two spines, one on each side, 0.055–0.068 mm; width including spines 0.059–0.074 mm; narrowest width 0.042–0.050 mm; a = 6.8–8.5, b = 3.3–4.0, V = 88.0–90.4%; length of esophagus 0.123–0.146 mm; vulva from anterior end 0.375–0.457 mm; egg 66.5×19.8 μ; body (Fig. 1) slightly curved, tapering slightly toward both ends; cuticle with 40–43 annules.

Head consisting of two annules, set off from body. First annule 22–28 μ in diameter, second, 19–23.5 μ. First annule with a row of spines directed slightly forward (Figs. 2, 3). Second annule with short spines. Head with six papillae: one large dorsal, one large ventral, and four small sublateral. Oral aperture oval. Each body annule bearing a row of spines, except those at the caudal end. First body annule 30–40 μ in diameter, including spines. Annules near middle of body each with about 70 spines, which vary somewhat in size and shape, some being short, some slender, some broad with distal ends outspread into a Y- or T-shape (Fig. 4). Generally, spines at middle of body about 6 or 7 μ long. Those near anterior end of body shorter and those toward posterior

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Contribution from the Nematology Section, Entomology Research Institute, Research Branch, Canada Department of Agriculture, Ottawa.

end longer. In front of each row of spines, a row of platelike structures (Figs. 2, 6). At caudal end spines on a few annules, sometimes on as many as nine, not in continuous rows (Fig. 5). Those annules with spatulate projections, each with several spines. Near the terminus, spines, few in number, usually two or three. Excretory pore on annule 11, 12, or 13, but more often on 12 (Fig. 6). Vulva 0.046–0.057 mm from posterior terminus, usually on seventh annule but sometimes on eighth. No spines around vulva, a platelike structure (Fig. 5) being found where spines usually are. Anal opening not determined. Spear (Fig. 2) 84.3 to 95 μ (with one exception, 100 μ) long, usually extending through eight body annules and occasionally through seven or nine. Basal knob large; at middle of median bulb, which is much larger than basal bulb. Dorsal gland orifice about 4.5 μ behind base of spear. Isthmus very short. Nerve ring crossing basal bulb and isthmus. Intestine a very broad tube, its wall clear and not granular. Rectum (Fig. 7) a narrow tube rising at about two or three annules behind vulva.

In young females the ovary extending to only about middle of body (Fig. 8). Oöcytes at proximal end arranged irregularly in two or more rows, followed by a few larger ones in a single row. Oviduct short. In very young females, cells on wall of region immediately behind oviduct not differentiated. Uterus slender, cells small. In more mature females, cells in anterior region of uterus large (Fig. 8), especially in older specimens (Fig. 7). Number of rows and number of cells in each row difficult to determine. Posterior region of uterus similar in young and older specimens. In older specimens, tip of ovary usually reaching esophageal region or even beyond median bulb, because of the rapidly developing ova. In one case, tip of ovary reaching second body annule. Ovary often reflexed, sometimes doubly reflexed.

Male.—Unknown.

Host.—*Saintpaulia* sp. (African violet).

Locality.—St. Laurent, Quebec, Canada.

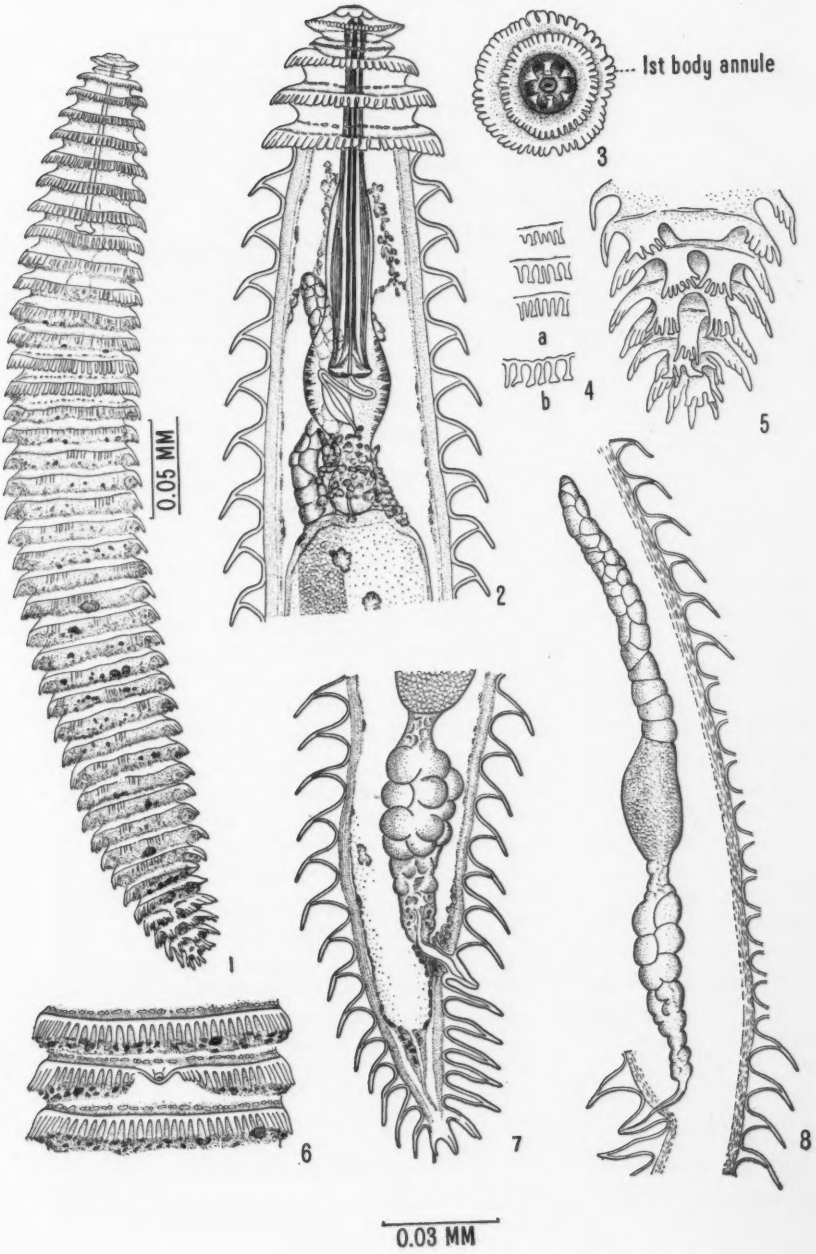
Holotype.—Canadian National Collection of Nematodes, No. 1475(2)*a*.

Paratype material.—Canadian National Collection of Nematodes, No. 1475(2).

Diagnosis

Criconema celetum, n. sp., under lower magnification, is easily mistaken for a species of *Criconemoides* because of the soil particles that collect under and around the spines and usually conceal them. *Criconema celetum* resembles *C. multisquamatum* and *C. fimbriatum* in having a transverse ring of spines on most of the annules and in the length of the spear. It differs from *C. multisquamatum* in having only two annules on the head; the first annule is similar to the second annule of *C. multisquamatum* in diameter but has a row of broad

FIGS. 1–8. Female of *Criconema celetum*, n. sp. 1. A mature specimen. 2. Anterior end, annules 4–12, optical section. 3. *En face* view, showing first head annule and first body annule. 4. (*a*) Spines on annules 12–14; (*b*) spines on annule more posterior. 5. Posterior end, ventral view. 6. Annules 11–13, ventral view. 7. Posterior end, optical section. 8. Reproductive system of young specimen with portion of body wall, optical section.


1st body annule
3
a
b
4
5
0.05 MM
1
2
6
7
8
0.03 MM

spines instead of merely "markings" as described by Kirjanova (2). *C. celetum* differs from *C. fimbriatum* in having fewer annules on the body and many more spines on each annule, and in not having the tip of the tail knob-shaped. This species differs from both *C. multisquamatum* and *C. fimbriatum* in the arrangement of spines at the caudal end.

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THE MINIMUM DOSAGE OF THIOUREA EFFECTIVELY INHIBITING THYROXINE SYNTHESIS IN THE FLOUNDER (PLATICHTHYS STELLATUS)[1]

J. E. KINNEAR[2]

Abstract

Thiourea in concentrations of 0.0025%, 0.005%, 0.01%, 0.02%, and 0.03% prevented the synthesis of thyroxine by the thyroid gland of the starry flounder (*Platichthys stellatus*). Concentrations of 0.001%, 0.0005%, and 0.0001% thiourea were not inhibitory. Concentrations of 0.005%–0.03% thiourea were effective for over 9 weeks. Flounder exposed to thiourea retained relatively little I^{131} in their thyroids. Although the synthesis of thyroxine was completely blocked by the inhibiting concentrations of thiourea, some synthesis of monoiodotyrosine and diiodotyrosine occurred.

Introduction

The thyroid in most bony fishes is a diffuse, non-encapsulated gland scattered about the ventral aorta (10). Hence, surgical removal is usually impossible, and other methods of promoting thyroid hormone insufficiency have been employed — in particular, chemical 'thyroidectomy' by several antithyroid drugs. Of the many compounds known to possess antithyroid activity, the thiocarbonamides (thiourea and its derivatives) have been most extensively employed with fish (13). These antithyroid compounds are believed to act on the thyroid by preventing the iodination of tyrosine, possibly due to the interference with the enzymatic oxidation of iodide to iodine (1).

The many experiments involving antithyroid drugs with fish have yielded rather conflicting and inconclusive results. In large measure, this is probably due to a lack of precise data concerning the minimum effective dose. It appears that this has never been carefully determined for fish and that the massive doses sometimes used may have had undesirable side effects. It is known that tissues other than those of the thyroid gland are sometimes affected, and side effects are not uncommon (4, 5, 9). In addition, the effects of prolonged treatment have not been carefully studied. There is always the possibility that an antithyroid drug may cease to be effective during a long-term experiment. Frieders (6) found this to be true for fish treated with phenylthiourea. Initially, inhibition of the thyroid was apparent but soon signs of a return to the euthyroid state were evident. Gish and Gatz (7) describe a similar condition with thiouracil on rats.

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In view of the situation outlined above, and, because these drugs are still extensively used in fish thyroid studies, the present investigation was undertaken to determine the effectiveness of thiourea in inhibiting synthesis of the thyroid hormones by a marine teleost. Experiments were followed for over 9 weeks to ascertain whether or not the thyroid gland would become refractory to thiourea.

Materials and Methods

Starry flounder (*Platichthys stellatus*) were collected locally at different times from January to June 1959. They were held in aerated aquaria containing 100 or 200 liters of sea water. Flounder were fed twice weekly on a mixture of horse heart and herring which had been ground to a suitable size. Specimens held for display purposes in the Vancouver Public Aquarium thrive on this diet.

Fish were immersed for 10- to 11-day periods in sea water solutions of thiourea (0.0001%, 0.0005%, 0.001%, and 0.0025%). Groups were also held for periods up to 60–74 days in concentrations of 0.005%, 0.01%, 0.02%, and 0.03%. Untreated control fish were maintained under similar conditions. During the course of the experiments, salinity of the water ranged from 20 $^0/_{00}$ to 27$^0/_{00}$ and the temperature from 10° to 12° C.

Flounder weighing from 25 to 300 g were injected with radioiodine 96 hours before they were to be killed. For example, fish to be killed after 10 days of treatment were injected on the sixth day of thiourea exposure. Carrier-free NaI^{131}, in tracer dosages of 20 or 25 μc, in a solution of distilled water (0.2–0.25 ml) was injected intraperitoneally with a 0.25-ml tuberculin syringe and 27-gauge needle. Two standards were made up representing 1/100 of the dose. Injected fish were always held in 100-liter aquaria and no food was offered following injection.

Fish were killed by bleeding. The thyroids were removed in the manner described by Hickman (11) and placed in steel planchets (25 mm × 7 mm) for counting. Counting was done by means of an end-probe scintillation counter using a $1\frac{1}{4}$ in. diameter × $1\frac{1}{2}$ in. thick NaI (Tl) crystal. Predetermined counts of 10,000 or 30,000 were recorded by a Philips scaler with the crystal 6 cm distant from the thyroid samples. Two standards were counted under the same conditions.

Extraction Procedures and Radiochromatography

The extraction method was a modified technique described by Roche *et al.* (14). The thyroids from a group of flounder (usually 10) were pooled, macerated, and digested with trypsin for approximately 72 hours at 40° C. The thyroid hydrolyzates were extracted 4 or 5 times with *n*-butanol, acidified to pH 1 to 2 with HCl. Extracts were combined and then evaporated over a water bath at a temperature not exceeding 40° C, until approximately 1 ml remained to be used for chromatography.

In some experiments, sera from treated fish and controls were extracted for labelled hormone. The blood collected from each fish was allowed to clot

in a 2-ml test tube, and the sera removed and pooled. Serum was extracted 5–6 times with acid butanol — the extractions treated in the same manner described for the thyroid.

Chromatography was by the ascending method using Whatman No. I or Whatman 3 MM. filter paper in sheets 33 cm × 23 cm. The solvent was a mixture of *n*-butanol, dioxane, and 2*N* NH_4OH in a 4:1:5 ratio shaken in a separatory funnel using the butanol phase as the solvent. The acid butanol extract was applied with a micropipette as a thin line 5 cm long, 4 cm from the base of the chromatograms in quantities ranging from 50 to 200 μl depending on the activity of the extract.

The rectangular glass chromatogram chamber was 30 cm × 25 cm × 40 cm. Chromatograms were saturated in the solvent vapors for at least 6 hours before they were dipped in the solvent. Development was overnight (12 to 14 hours), the solvent travelling approximately 25 cm. On removal of the chromatogram from the chamber, the solvent front was marked and the chromatogram prepared for autoradiography. Details of the technique for paper chromatography were based on Block *et al.* (2).

Ilford no-screen X-ray films 30 cm × 25 cm individually packed in light proof envelopes were found convenient for autoradiography. Film and chromatogram, with a thin sheet of cellophane between, were placed together and sealed in the film envelope. The envelopes were placed between two weighted sheets of glass and left for a period of 8 days or longer. Films were developed by routine methods.

On each chromatogram, synthetic thyroxine (Na salt) which was "tagged" with I^{131} by the method of Gleason (8), was applied in 20-μl quantities to act as a reference point for the identification of natural thyroxine synthesized by the gland. In addition, after the autoradiogram was developed, the chromatogram was sprayed with diozotized sulphanilic acid followed by ½ saturated Na_2CO_3. The resulting pink and purple spots were matched with the darkened areas of the autoradiogram. Synthetic monoiodotyrosine and diiodotyrosine with the sulphanilic acid spray test established the position of these compounds on the chromatograms and thus served to identify natural mono- and diiodotyrosine.

Results

The results (Table I) show that thiourea in concentrations of 0.0025%, 0.005%, 0.01%, 0.02%, and 0.03% effectively prevented the synthesis of thyroxine, while lower concentrations (0.0001%, 0.0005%, and 0.001%) did not abolish this synthesis. In those concentrations (0.005%–0.03%) in which flounder were exposed to thiourea for over 9 weeks, no "escapement" occurred. The thyroids of flounder remained inhibited during this prolonged course of the treatment. Typical autoradiograms are shown in Fig. 1.

Table II shows that flounder exposed to inhibiting concentrations (0.0025% and higher) of thiourea retained a relatively low percentage of the injected dose of radioiodine in the thyroid. In contrast, controls had substantially

higher values and those groups exposed to the non-inhibiting concentrations of thiourea (0.001% and lower) had percentage dosages similar to those of the controls. Some exceptions were noted. About 10% of the treated fish in concentrations 0.0025% and above had percentage dosages in the gland equal to or above the controls. Such cases were always analyzed for thyroid hormones separately, but *in no case was labelled thyroxine detected.* Thyroxine could always be detected in a single fish used as a control (no thiourea treatment).

TABLE I

Summary of analyses of thyroid glands of groups of starry flounder exposed to thiourea

Thiourea, %	Duration of treatment, days	Result*
0.03	63,74	+
0.02	32,69	+
0.01	32,61,69	+
0.005	11,12,32,69	+
0.0025	11	+
0.001	10	−
0.0005	10	−
0.0001	10	−

*+, thyroxine synthesis inhibited; −, no inhibition of thyroxine formation.

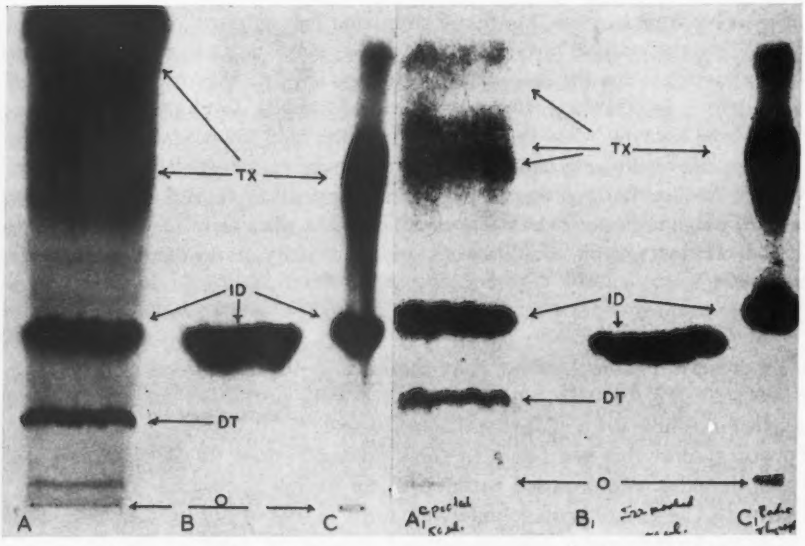

FIG. 1. Radioautographs of chromatograms of extracted thyroids from fish injected with tracer I^{131}. A and A_1, control fish not exposed to thiourea; B (left series), fish exposed to 0.03% thiourea for 63 days, B_1 (right series), 0.02% thiourea for 61 days, C and C_1, synthetic thyroxine "tagged" with I^{131}; O, origin; DT, diiodotyrosine; ID, inorganic I^{131}; TX, thyroxine; solvent, *n*-butanol, dioxane, and 2*N* NH_4OH.

TABLE II

Uptake of I^{131} by thyroids of fish which had been immersed in solutions of thiourea for 10 days or longer, expressed as mean and standard deviation for percentage uptake of the injected doses of radioiodine by the different thyroids counted

Thiourea in ambient solution (%)	Thyroids counted (n)	% uptake of I^{131}	
		Mean	Standard deviation (σ)
0	43	4.6	2.0
10^{-3} to 10^{-4}	28	5.0	2.7
5×10^{-4}	10	4.9	2.4
25×10^{-4}	13	0.7	0.3
5×10^{-3}	38	0.8	0.6
2 to 3×10^{-2}	31	0.9	0.7

Autoradiograms generally revealed that inorganic iodide was the only radioactive substance in the thyroid of fish exposed to 0.0025% and higher concentrations. However, traces of monoiodo- and diiodo-tyrosine were detected on autoradiograms of groups of fish exposed to 0.005%, 0.01%, and 0.02% for 32 days suggesting that synthesis of the lower iodinated analogues occurred very slowly during inhibition. No trace of thyroxine was evident.

Serum Analyses

Serum was extracted and autoradiochromatographed for thyroid hormones in those groups of fish exposed to 0.005%, 0.01%, and 0.02% thiourea for 32 days, and for groups exposed to the same concentrations for 69 days. No thyroid hormones were detected, although thyroxine was detected in sera from controls which were not exposed to thiourea.

Discussion

The lowest effective dose of thiourea (0.0025%) is a decidedly lower concentration than normally used by fish physiologists. Pickford and Atz (13) state that a widely used concentration of thiourea has been 0.03%–0.033% (about 12 times higher than 0.0025%). Concentrations of 0.05% (20 times) and 0.1% have also been used. Several investigators have used concentrations lower than 0.03%. For example, Lever *et al.* (12) treated *Lebistes reticulatus* with 0.01% thiourea and noted hypertrophy and hyperplasia of the thyroid. Buser-Lahaye (3) used 0.02% on *Gambusia affinis* and likewise noted a response. Whether or not the very low concentrations of thiourea found effective in this study (0.0025% in particular) will prove to be effective on all species of fish remains to be demonstrated.

Thiourea studies on the starry flounder strongly suggest that escapement by the thyroid over a period of time is unlikely. There were no signs of a return to normal thyroid function during the 9 week experiment. The lowest concentration (0.0025%) was followed for only 11 days, but Hickman (personal communication) using this concentration up to 40 days, found it to be effective.

A fish exposed to inhibiting concentrations of thiourea almost invariably showed weak radioiodine trapping activity by the thyroid gland. This relation could prove to be a useful and convenient way for assessing inhibition. The exceptions to the general rule that low uptake at 96 hours signifies inhibition are difficult to explain. There was a tendency for this to occur more often in the long term experiments. Perhaps a failure to excrete the dose of I^{131} at the normal rate resulted in greater accumulation.

In the thyroxine-inhibited fish, presence of monoiodotyrosine and diiodotyrosine was the exception rather than the rule. These lower analogues appeared at 32 days of treatment from fish exposed to 0.005%, 0.01%, and 0.02%. Labelled thyroxine was not present. The analogues were not detected in the pooled serum of these groups. It would appear that some organic synthesis of these lower analogues occurs slowly in the thyroids of fish exposed for a long time to thiourea. Since, however, they were not detected in the serum, their physiological importance to the fish is questionable.

Acknowledgments

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THE METAZOAN PARASITES OF THE HETEROSOMATA OF THE GULF OF ST. LAWRENCE

VI. DIGENEA[1,2]

KEITH RONALD[3]

Abstract

Aporocotyle simplex, Brachyphallus crenatus, Cryptocotyle lingua, Derogenes varicus, Genolinea laticauda, Gonocerca crassa, Hemiuris appendiculatus, H. communis, H. levinseni, Hemiuris sp., *Lepidapedon rachion, Otodistomum veliporum, Peracreadium commune, Plagioporus varia, Podocotyle atomon, P. olssoni, Prosorhynchus squamatus, Steganoderma* (*Steganoderma*) *formosum, Stenakron vetustum, Stephanostomum baccatum, Steringophorus furciger, Steringotrema cluthense,* and *S. pagelli* were identified in a study of 560 specimens of Heterosomata (*Hippoglossoides platessoides, Hippoglossus hippoglossus, Limanda ferruginea, Liopsetta putnami, Pseudopleuronectes americanus,* and *Scophthalmus aquosus*) from the Gulf of St. Lawrence area. Host distribution is indicated, together with parasitic incidence.

Introduction

The digenetic trematodes of fish of the North Atlantic are fairly well known, with the exception of the semienclosed waters, such as the Gulf of St. Lawrence. In this paper the Digenea of the flatfish of the Gulf are briefly described. Their distribution and that of their hosts are given.

In general, the variety of species is not great, as only 22 species representing 17 genera were found, whereas there are records of over 150 species in the literature (20). It should be noted that these trematodes represent nine families, indicating that there is no apparent sign of specificity either at trivial or higher levels. The rate of infection by some intermediate stages of these trematodes, however, is high enough to produce a pathological condition.

Methods

The fish used in this study were taken by means of otter and beam trawl, long and hand line, purse and Danish seine, cod trap, herring and cod gill net, beach seine, and even the lobster trap.

The fish were examined externally, and counts made of the metacercariae inevitably present on the fin and body surfaces of the fish. The fish were opened, the digestive tracts tied off, behind the stomach, caeca, first, second, and last third of the intestine. In some cases, as in the halibut and witch, the intestinal mucus made it impossible to see the smaller parasites. In order to remove or break down this mucus, the contents of the section of the intestine were placed in a blender, with about 10 times their volume of 0.1% aerosol in water. The blender was run for 30 seconds at slow speed, the contents were

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[2]No. 75, Contributions du Département des Pêcheries.
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then allowed to settle for an hour. After this period most of the mucus had accumulated at the top, where it was easily removed by skimming with a filter paper. The mucus was thoroughly washed through a series of sieves so that any specimens that had been held in suspension were visible. The parasites were removed from the bottom of the blender jar at which time they were clear of any mucus.

The trematodes were allowed to relax overnight in a solution of 1 part of sea water and 2 parts of distilled water. They were then fixed in Gilson's (1898) fluid for at least 1 day, then washed for the same period. The trematodes were either stained with dilute Mayer's carmalum (21) or with Grenacher's alcoholic borax carmine or Best's (1906) carmine. After dehydration and clearing the specimens were mounted; no attempt was made to apply pressure as distortion and displacement of the internal organs occur. This can result in a description of a new species based purely on bad technique.

Suborder GASTEROSTOMATA Odhner, 1905

Family BUCEPHALIDAE Poche, 1907
Subfamily PROSORHYNCHINAE Nicoll, 1914
Genus *Prosorhynchus* Odhner, 1905

Prosorhynchus squamatus Odhner, 1905
Host: Hippoglossus hippoglossus.
Location: Stomach and intestine.
Locality: East Point, Anticosti Island.

Two specimens were taken on May 30, 1955, from one halibut, captured on a long line at depth of 72 meters. Stafford (24) recorded *Gasterostomum armatum* Molin from the halibut; Odhner (18) stated that *G. armatum* of Molin, 1861 differs from *G. armatum* of Olsson, 1868 and Levinsen, 1881. Odhner pointed out that *Gasterostomum armatum* of Molin was synonymous with *Monostomum crucibulum* Rudolphi, 1819. He therefore created a new genus *Prosorhynchus* with the genotype *Prosorhynchus squamatus*. The present survey substantiates Stafford's record that this trematode is a parasite of the halibut in Canadian waters; it has also been reported as a pseudoparasite of *Squalus acanthias* (14).

The two specimens examined were young adults, one of which had several eggs in the uterus. The length was 0.80 to 1.10 mm with a width of 0.35 to 0.48 mm.

Suborder PROSOSTOMATA Odhner, 1905

Family FELLODISTOMATIDAE Odhner, 1911
Subfamily FELLODISTOMATINAE Odhner, 1911
Genus *Steringophorus* Odhner, 1905

Steringophorus furciger (Olsson, 1868)
Hosts: Glyptocephalus cynoglossus; Hippoglossus hippoglossus; Limanda ferruginea; Liopsetta putnami; Pseudopleuronectes americanus.

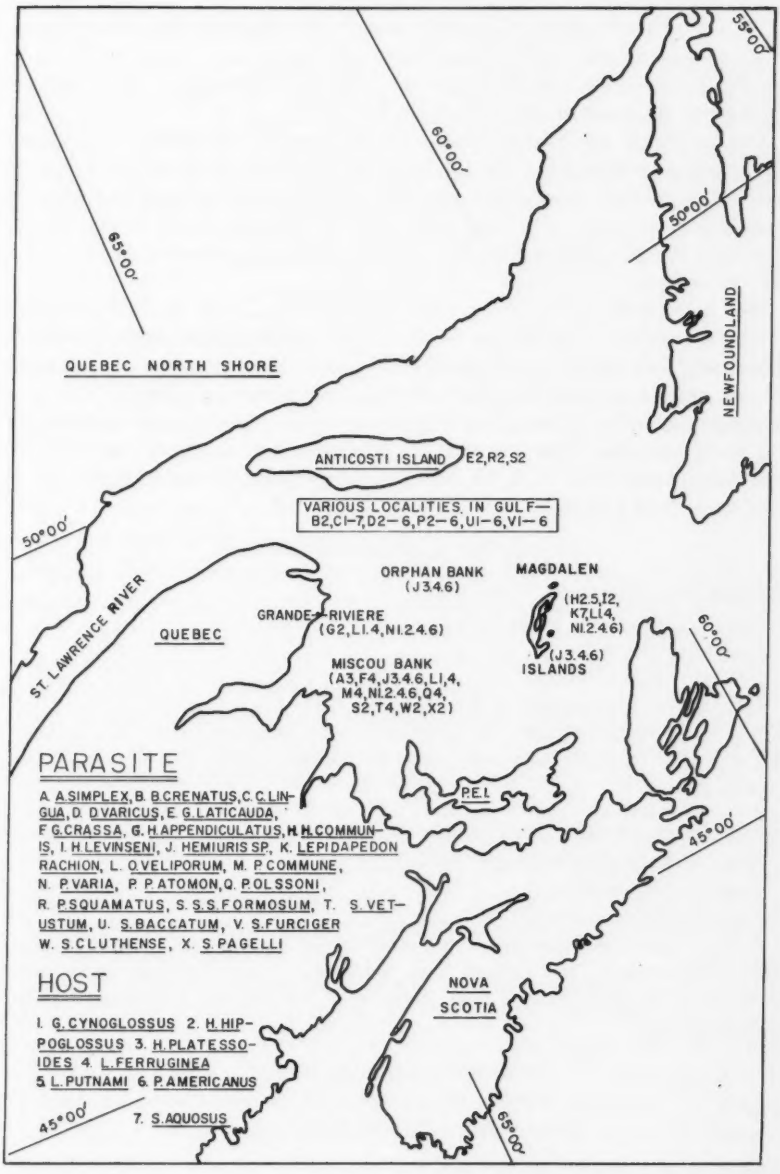

FIG. 1. Distribution of the digenetic trematodes of the Heterosomata in the Gulf of St. Lawrence.

Location: Stomach—*G. cynoglossus, L. ferruginea.*
Pyloric caeca—*G. cynoglossus, H. hippoglossus, Limanda ferruginea, Liopsetta putnami, P. americanus.*
Intestine—*H. hippoglossus, Limanda ferruginea, P. americanus.*
Locality: All parts of the Gulf of St. Lawrence.

The incidence of *Steringophorus furciger* varied markedly in individual specimens, as well as between different species. The yellowtail (*L. ferruginea*) carried the greatest number of parasites, one specimen harbored 98 trematodes in its digestive tract. The least number of *S. furciger* found in any one was five. The incidence figure was 86% for the yellowtail flounder, 25% of which were immature.

This trematode was found in the witch in 70% of the witch examined, in numbers varying from one to four. The immature flukes made up 80% of this number. In the smooth flounder 70% of the fish examined were parasitized by one or two trematodes, all of which were mature specimens. The winter flounder was lightly infested; in 4% of the sample, only a single mature worm was found in each of the four fish. This parasite was easily recognizable from previous descriptions (6, 9, 13, 18). The shape was highly variable and was very dependent on the method of fixation.

Genus *Steringotrema* Odhner, 1911

Steringotrema cluthense (*Nicoll, 1909*)
Host: Hippoglossus hippoglossus.
Location: Stomach.
Locality: Miscou Bank.

This is the first record of this parasite from the halibut; it was found in only one of the fish examined. Only two of these trematodes were present in the stomach; identification was made by consulting the description given by Dawes (2).

Steringotrema pagelli (Van Beneden, 1870)
Host: Hippoglossus hippoglossus.
Location: Intestine.
Locality: Miscou Bank.

A single specimen was found in a small halibut taken in 18 meters of water. This is a new record for this fish. The presence of a large ventral sucker, almost three times the diameter of that of the oral, indicated the parasite's position in this species.

Family ALLOCREADIIDAE Stossich, 1904
Subfamily LEPOCREADIINAE Odhner, 1905
Genus *Lepidapedon* Stafford, 1904

Lepidapedon rachion Cobbold, 1858
Host: Scophthalmus aquosus.
Location: Intestine.
Locality: Pleasant Bay, Magdalen Islands.

This is the first record of *L. rachion* in any flatfish; the hosts recorded previously have all been gadoids.

The long ribbon-like shape, long prepharynx, and short oesophagus distinguished this genus from any other in the subfamily. Its length was 3.2 mm with a breadth of 0.74 mm; this ratio of length to width placed it in the species *L. rachion* rather than *L. elongatum*, in which the length is greater in proportion to its width. The species is well described by Dawes (3). It was present in 2% of the fish examined only as a solitary specimen.

Subfamily ALLOCREADIINAE Looss, 1902
Genus *Podocotyle* (Dujardin, 1845)

Podocotyle atomon (Rudolphi, 1802)

Hosts: *Hippoglossoides platessoides*; *Hippoglossus hippoglossus*; *Limanda ferruginea*; *Liopsetta putnami*; *Pseudopleuronectes americanus.*

Location: Intestine—*Hippoglossoides platessoides*; *Hippoglossus hippoglossus*; *Limanda ferruginea*; *Pseudopleuronectes americanus.*
Caeca—*Limanda ferruginea.*
Stomach—*Limanda ferruginea*; *Liopsetta putnami.*

Locality: Gulf of St. Lawrence.

Podocotyle atomon has been noted for its morphological variations; this fact has caused several new species to be described in the literature, which have later fallen into synonymy with *P. atomon.* In the present survey over 400 specimens were examined; the measurements of these were wide enough in range to include three other described species.

The highest incidence was in the yellowtail, where 50% of the fish were parasitized by *Podocotyle atomon.* The numbers present varied from 1 to 21 parasites per fish; 20.6% of which were immature. In the winter flounder parasitism occurred in 14% of the fish studied; there were one to nine trematodes in the intestine, only 3% of which were immature. The plaice showed an incidence figure of 7%; there were from 2 to 20 trematodes in each fish. The incidence in the halibut was 10%, with a maximum of two parasites per fish. The smooth flounder had a parasitic incidence of 20%; a single trematode was found in each specimen.

The description of those specimens of *P. atomon* examined is as follows: The length is 1.5 to 3.5 mm and the width 0.47 to 0.89 mm. The oesophagus is usually longer than the pharynx. The vitellaria run laterally; they are follicular and well developed, and they may or may not fill the intertesticular space. The testes are tandem and measure at least half the width of the body. The presence of the trilobed ovary was not used taxonomically, as some specimens of *P. atomon* were found to have two or even four lobes present.

The presence of *Podocotyle atomon* in *Hippoglossoides platessoides* and *Liopsetta putnami* is reported here for the first time, whereas it has been reported previously from *Raja ocellata* (14).

Podocotyle olssoni Odhner, 1905

Host: Limanda ferruginea.

Location: Caeca.

Locality: Miscou Bank.

P. olssoni was found with *P. atomon* in the caeca of a medium-sized yellowtail flounder captured at a depth of 18 meters. *L. furruginea* carried 16 of these parasites, all of which were mature. Heller (4) expresses some doubt as to the validity of the species, suggesting that they may be "strongly contracted specimens of *P. reflexa*". The measurements made on living specimens did not substantiate her hypothesis. The extended length of the living worms was 3.90 mm, 2.95 mm upon contraction. The width was from 0.42 mm when contracted to 0.34 mm when extended. The testes were less than half the width of the body in the extended parasite. The oral sucker's width was slightly less than that of the ventral. The oesophagus was usually shorter than the pharynx.

P. olssoni has been reported as a parasite of *L. ferruginea* from North Carolina and Massachusetts (7, 8) so that the present record extends the range of this parasite northwards.

Genus *Plagioporus* Stafford, 1904

Plagioporus varia (Nicoll, 1910)

Hosts: Glyptocephalus cynoglossus; *Hippoglossus hippoglossus*; *Limanda ferruginea*; *Pseudopleuronectes americanus.*

Location: Pyloric caeca of *L. ferruginea.*
Intestine of *G. cynoglossus* and *P. americanus.*

Locality: Miscou Bank; Grande-Rivière; Magdalen Islands.

Plagioporus varia was represented by a single specimen in three of the four hosts; four specimens of *L. ferruginea* carried this parasite, two of *P. americanus*, and only one specimen of *G. cynoglossus* was parasitized. The halibut was found to carry from one to seven parasites in 15 fish.

The trematodes from the halibut closely resemble those classified by Yamaguti (31) as *Plagioporus* (*Caudotestis*) *nicolli*, but Dawes (2) stated that "Issaitchikow (5) proposed the erection of the subgenera *Caudotestis*, *Mediantestis* and *Lebouria*, with the types *nicolli* n.sp., *tumidula* and *idonea* respectively, an apparently unnecessary procedure as regards British species." The specimens examined from the flatfish also lacked enough morphological differences to require subgeneric division.

The trematodes measured from 1.15 to 1.34 mm in length by 0.48 to 0.61 mm in width. The oral sucker was circular, 0.17 mm in diameter, the ventral sucker was wider than long (0.325 to 0.260 mm). The eggs were bluntly pointed at both ends and measure 0.069 to 0.078 mm in length and 0.040 to 0.050 mm in width. All of the fish noted above are new host records for this parasite.

Genus *Peracreadium* Nicoll, 1909

Peracreadium commune (Olsson, 1867)

Host: Limanda ferruginea.

Location: Pyloric caeca.

Locality: Miscou Bank.

A single specimen of *P. commune* was found in one yellowtail flounder. Linton (7) reported this parasite from *P. americanus*, but did not find it in *L. ferruginea*. This present material, therefore, represents the first record of this parasite in the yellowtail. It has been suggested that this species is synonymous with *Peracreadium genu* (3). The specimen taken was 1.80 mm in length, with a pharynx measuring 0.135 mm long by 0.091 mm wide. The presence of the spindle-shaped pharynx determined the parasites specific position.

Stenakron vetustum Stafford, 1904

Host: Limanda ferruginea.

Location: Intestine, close to the anus.

Locality: Miscou Bank.

This parasite was found in 14% of the *L. ferruginea* examined in numbers of from 2 to 31, over half of these were young with few if any eggs in the uterus.

Linton (7) was the first to record this species but did not name it; his host was the same as in the present material. Miller (13) in reviewing Stafford's material states that "In the one specimen in which the ovary can be seen clearly it consists of three separate and distinct oval parts. Thus there are apparently three ovaries." His observation was interesting but incorrect; the ovary is made up of from two to four lobes which are joined by very fine tubular connections; these are not apparent in poorly stained specimens.

The trematode measures from 1.30 to 1.75 mm in length and 0.70 to 0.95 mm in width. The oral sucker has a diameter of from 0.13 to 0.21 mm, the acetabulum from 0.25 to 0.32 mm. The testes are irregularly shaped; the ovary may be partially surrounded by the posterior testis.

Family ACANTHOCOLPIDAE Lühe, 1909

Genus *Stephanostomum* Looss, 1899

Stephanostomum baccatum (Nicoll, 1907)

Hosts: Glyptocephalus cynoglossus; *Hippoglossoides platessoides*; *Hippoglossus hippoglossus*; *Limanda ferruginea*; *Liopsetta putnami*; *Pseudopleuronectes americanus.*

Location: Metacercariae on body surfaces, musculature, branchial and oral cavities. Adults in pyloric caeca and intestine.

Locality: Gulf of St. Lawrence.

The metacercarial form of *Stephanostomum baccatum* is one of the commonest trematode parasites of the Heterosomata in the Gulf. The encysted parasite was found on every flatfish studied; the greatest number found was 527.

Scophthalmus aquosus was the most heavily parasitized of all the flatfish. The most highly parasitized specimens of this species were taken in the shallow waters of the lagoons at the Magdalen Islands. Wolfgang (26, 27, 28, 29) recently completed a survey of these parasites in Canadian waters. A discrepancy occurs between his incidence figures (26) and those of the present survey; he indicates low incidence in the fish from the Baie-des-Chaleurs area. Although his sampling was carried out on the south side, it is not felt that any great difference in incidence should be found in the 26-mile width of this bay. The small fish of all species in this area were invariably infected with *Stephanostomum baccatum* metacercariae, not, as he stated, just in a few cases with small numbers of parasites. In 15 of the halibut examined, *Stephanostomum baccatum* cysts were found free in the intestine. Young adults were removed from the outside of the stomach wall of *Pseudopleuronectes americanus*, *Hippoglossus hippoglossus*, and *Limanda ferruginea*. These trematodes were, in some cases, still encysted but had all the characteristics of the adult worm. The oral spines were not always present in their full number; if lacking, they were replaced by the small, rounded pubescent spines (28).

The only specimens of *Stephanostomum baccatum* found bearing eggs were those taken from the halibut. The halibut captured close to Anticosti Island were parasitized by from 3 to 11 specimens; the fish from Magdalen Island always carried a single specimen. In all, 12 of the fish were found to harbor *S. baccatum*.

Wolfgang (29) divided the species recorded by Caballero (1) into five groups dependent on the shape and size of the vitellaria. This table, listing the species with their respective differences in morphology, was a useful taxonomic guide.

The length of the adult trematode in the halibut was from 2.05 to 2.75 mm, with a width at the acetabulum of 0.425 to 0.475 mm, at the posterior testis 0.540 to 0.680 mm. The oral sucker, measured from the anterior extremity to the base of the oral spines, had a length of 0.069 to 0.082 mm and a width of 0.180 to 0.220 mm. The acetabulum is circular, having a diameter of from 0.280 to 0.320 mm. The eggs are 0.062 to 0.064 mm long by 0.033 to 0.035 mm wide.

The vitellaria is uninterrupted, and the cirrus short and unarmed. The body is spined, and the spines decrease in size posteriorly, the spination ending at the level of the posterior limit of the vitellaria.

Family ZOOGONIDAE Odhner, 1911
Genus *Steganoderma* Stafford, 1904

Steganoderma (Steganoderma) formosum Stafford, 1904

Host: Hippoglossus hippoglossus.

Location: Pyloric caeca and intestine.

Locality: Miscou Bank; East Point, Anticosti Island.

Yamaguti (30) divided the genus *Steganoderma* into the two subgenera *Steganoderma* and *Lecithostaphylus*. Miller (13) doubted Manter's (11) differentiation of the one genus into the two genera *Steganoderma* (for Stafford's (23) material) and *Lecithostaphylus* of Odhner (19). The division at subgeneric

level is more acceptable, as the differences between the two subgenera are not marked enough to classify them at a higher level. This species has been reported as a pseudoparasite of *Raja laevis* and *Squalus acanthias* from the Gulf (14).

Stafford's (23) original description indicates spination of the body; one specimen in the present survey lacked body spines. However, three other specimens, taken from another fish, had spines. The specimens taken measured 2.50 to 3.05 mm in length by 0.65 to 0.75 mm in width. The spines were larger at the anterior end of the body. The oral and ventral suckers were circular and of the same size, with a diameter of 0.22 mm. The eggs were 0.030 to 0.039 mm long by 0.012 to 0.020 mm wide.

Family AZYGIIDAE Odhner, 1911
Genus *Otodistomum* Stafford, 1904

Otodistomum veliporum (Creplin, 1837)

Hosts: Glyptocephalus cynoglossus; *Limanda ferruginea.*

Location: Digestive tract, liver, gonads.

Locality: Miscou Bank; Grande-Rivière; Magdalen Islands.

Heller (4) reviewed the literature concerning the genus *Otodistomum* and described *O. cestoides* from *Raja scabrata*; she was uncertain as to the correct trivial name for this parasite. Myers has recorded this trematode from *Raja ocellata*, *R. radiata*, and *Squalus acanthias* (14). Dawes (3), in a comprehensive review of the genus, makes *O. cestoides* synonymous with *O. veliporum*. He also states "The distinction put forward by Odhner for the separation of *O. cestoides* and *O. veliporum* is useless."

The metacercariae of *Otodistomum* have been found previously in the witch (16, 22). The presence of larval *O. veliporum* in *Limanda ferruginea* forms a new host record.

In one of the yellowtail flounders, the intestinal tract, body cavity, and perianal region were covered with approximately 500 cysts of this parasite. In studying these trematodes, it was noted that the body was often rigid and in a "petrified" state, brittle to the touch and yellowish in color. The cyst contained a granulated white fluid, in which the worm was bathed. It was obvious that many of the trematodes were dead, perhaps due to the strong host reaction of this fish.

O. veliporum was present in 6% of the specimens of *Limanda ferruginea* examined.

In the witch, the parasite was usually found in a viable condition, the specimens attained a length of 2.30 mm and a width of 1.10 mm. The suckers differed in size with the ventral being the larger, 0.80 mm, in diameter; the oral was 0.52 mm in diameter. The excretory vessel is Y-shaped and extended anteriorly to the sides of the oral sucker.

The parasites were often found between the muscle fibers of the gut wall, and they even protruded into the lumen.

O. veliporum was present in 80% of the witch examined, the number of specimens present ranging from 1 to 27.

Family HEMIURIDAE Lühe, 1901
Subfamily HEMIURINAE Looss, 1907
Genus *Hemiuris* Rudolphi, 1809

Hemiuris communis Odhner, 1905

Hosts: Hippoglossus hippoglossus; *Liopsetta putnami.*

Location: Stomach.

Locality: Magdalen Islands.

H. communis was found in 2% of the specimens of *L. putnami* examined, always as a solitary specimen. In the halibut, 25% of the fish carried from one to five parasites. The length of the soma in these specimens was from 1.54 to 1.82 mm, the breadth 0.30 to 0.54 mm. The modal length of 67 specimens taken from both hosts was 1.63 mm, the width 0.39 mm. The length to the width was in the ratio of 4 to 1.

The oral sucker measured from 0.14 to 0.22 mm in length and 0.16 to 0.22 mm in width. The modal diameter was 0.18 mm. The pharynx was 0.108 to 0.154 mm long by 0.011 to 0.012 mm wide. The ventral sucker was spherical with a diameter of 0.18 to 0.40 mm; the mean was 0.26 mm. The oral sucker and the ventral sucker are in the ratio of 7:9. The eggs were 0.020 to 0.039 mm in length by 0.009 to 0.020 mm wide.

The trematodes were striated on the ventral surface to the level of the ecsoma; in the region of the oral sucker, there was slight striation of the dorsal surface.

Hemiuris levinseni Odhner, 1905

Host: Hippoglossus hippoglossus.

Location: Stomach.

Locality: Magdalen Islands.

Manter (11) gave the diagnostic characteristic for this species as the equal size of the two suckers. In some of the specimens taken in this survey, the oral sucker was found to be slightly larger than the ventral. The original description of this species indicated that this difference may occur (18).

A single specimen was taken from the halibut. This parasite is quite common in the waters of the Gulf, but as a parasite of *Gadus callarias* (4), *Raja laevis*, and *Squalus acanthias* (14).

Hemiuris appendiculatus (Rudolphi, 1802)

Host: Hippoglossus hippoglossus.

Location: Stomach.

Locality: Grande-Rivière.

Linton (9) has described specimens found in fish of the Woods Hole region, the specimens recorded here agree closely with his material. The number of parasites found varied from 1 to 49, only 4% of the halibut harbored *H. appendiculatus.*

The comparative size of the ventral sucker in the present material placed the specimens within the species. The oral sucker measured 0.21 mm, while the ventral sucker was 0.347 mm in diameter.

Hemiuris sp.

Hosts: Hippoglossoides platessoides; *Limanda ferruginea*; *Pseudopleuronectes americanus.*

Location: Stomach of *L. ferruginea.*
Intestine of *L. ferruginea*, *H. platessoides*, and *P. americanus.*

Locality: Miscou Bank; Le Fond George, Magdalen Islands; Orphan Bank.

A few specimens were found either encysted or free in the stomach and intestine of the hosts; the presence of paired vitellaria placed them in the genus *Hemiuris*, but the development of the other internal organs was not complete. The ecsoma was contracted in all specimens; the length of the soma was 2.40 mm, the suckers were almost identical in size, with a slight bias towards an increase in the size of the acetabulum.

The incidence of *Hemiuris* sp. was one parasite in four of the yellowtail, two to six in three specimens of the winter flounder, and five parasites in one plaice.

Genus *Gonocerca* Manter, 1925

Gonocerca crassa Manter, 1934

Host: Limanda ferruginea.

Location: Stomach.

Locality: Miscou Bank.

This is not an unusual parasite of the Heterosomata (12) but the present material forms a new host record. Twenty-one specimens were found in the stomach of a yellowtail flounder.

The position of the testes in the hind body, and the pretesticular position of ovary, together with the lack of filaments on the eggs were the criteria used in identifying these specimens.

Genus *Genolinea* Manter, 1925

Genolinea laticauda Manter, 1925

Host: Hippoglossus hippoglossus.

Location: Stomach.

Locality: East Point, Anticosti Island.

A single specimen was found in the stomach of a small halibut which was taken in 3.5 meters of water. Manter (10) described this species from the halibut in the waters of the coast of Maine. The present record extends the geographical limits of this parasite northwards.

The dimensions of the specimens closely followed the description of Manter, the vitellaria were situated behind the ovary, the intestinal caeca reached the posterior extremity of the body, and the uterus coiled back to the level of the vitellaria.

Subfamily DEROGENETINAE Odhner, 1927
Genus *Derogenes* Lühe, 1900

Derogenes varicus (Müller, 1784)

Hosts: Hippoglossoides platessoides; *Hippoglossus hippoglossus*; *limanda ferruginea*; *Liopsetta putnami*; *Pseudopleuronecetes americanus.*

Location: Stomach of *L. putnami.* Stomach and intestine of *H. platessoides* and *P. americanus.*

Stomach, intestine, and caeca of *H. hippoglossus* and *L. ferruginea.*

Locality: Gulf of St. Lawrence.

The cosmopolitan parasite *D. varicus* was well represented in the flatfish of the Gulf. All the yellowtail flounders carried this parasite, in numbers ranging from 1 to 112; 45% of the halibut harbored from 1 to 44 trematodes. The winter flounder was lower in incidence with 10% of the fish having 1 to 28 trematodes. Seven per cent of the plaice were parasitized by from one to eight trematodes. The smooth flounder, *L. putnami,* was lightly infected, with 4% of the fish having one or two trematodes in their stomachs. All the specimens found in the plaice and the smooth flounder were immature, while the halibut carried only mature trematodes. Ten per cent of the trematodes in the winter flounder, and 16.7% of those in the yellowtail, were immature.

The specimens were typical of those previously described (3, 15, 18). The cuticle was annulated dorsally to the posterior extremity of the mouth, and the mouth was partially overhung by a lip. The modal measurements of 1000 specimens was noted. The length of the trematode was 2.20 mm, the width 0.45 mm. The oral sucker is smaller than the ventral, 0.28 by 0.24 mm and 0.44 by 0.44 mm respectively. The eggs were 0.054 mm in length by 0.030 mm in width.

Subfamily STERRHURINAE Looss, 1907
Genus *Brachyphallus* Odhner, 1905

Brachyphallus crenatus (Rudolphi, 1802)

Host: Hippoglossus hippoglossus.

Location: Stomach and intestine.

Locality: Gulf of St. Lawrence.

This parasite was present in 50% of the halibut examined, in numbers varying from 1 to 112. Those halibut that carried a great number of *B. crenatus* were taken in the waters of the Magdalen Islands. Only four specimens were found in the intestine; thus the stomach appears to be the favored site of infection.

Miller (13) in his revision of Stafford's (23) material found that the 12 specimens described as *Hemiuris appendiculatus* by Stafford were in reality *B. crenatus.* The halibut was listed by Stafford as one of the hosts for his *Hemiuris appendiculatus.* This present work, therefore, forms the second record of *Brachyphallus crenatus* from this host.

The specimens measured 1.35 to 1.95 mm in length and 0.27 to 0.39 mm in width. The ventral sucker was the larger, 0.15 to 0.20 mm, while the oral was 0.14 to 0.18 mm. The eggs measured 0.020 to 0.025 mm long by 0.010 to 0.016 mm wide.

These specimens were smaller than those described by Heller (4) from fish taken in the Baie-des-Chaleurs; this is to be expected as variation does exist in specimens from different hosts (3). Heller's material was taken from *Clupea harengus*, *Osmerus mordax*, and *Salmo salar*.

Family APORCOTYLIDAE Odhner, 1912
Genus *Aporocotyle* Odhner, 1900

Aporocotyle simplex Odhner, 1900

Host: Hippoglossoides platessoides.

Location: Intestine.

Locality: Miscou Bank.

A single specimen was found in the intestinal mesentery of a plaice. The host was 37 cm in length and taken in an otter trawl at a depth of 36 meters. This is a new host record for *A. simplex*, and also the first time it has been found in North American waters.

The parasite measured 3.80 mm in length and 0.57 mm in width. The cuticle carried spines, the largest of which were on the ventral surface, in groups of 11 to 17. The number of testes present in this specimen was 143 (a greater number than previously recorded (17)). The ovary is oval with a small indentation on the anterior edge; the length is 0.15 mm, and the width 0.20 mm.

The vitellaria is well developed and follicular, limited posteriorly at the posterior extremity of the ovary. This specimen of *A. simplex* was not found to have eggs present in the uterus.

Family HETEROPHYIDAE Odhner, 1914
Subfamily CRYPTOCOTYLINAE Lühe, 1909
Genus *Cryptocotyle* Lühe, 1899

Cryptocotyle lingua (Creplin, 1825)

Hosts: Glyptocephalus cynoglossus; *Hippoglossoides platessoides*; *Hippoglossus hippoglossus*; *Limanda ferruginea*; *Liopsetta putnami*; *Pseudopleuronectes americanus*; *Scophthalmus aquosus.*

Location: Body surface, and inside of all external orifices.

Locality: Gulf of St. Lawrence.

The highest incidence of *C. lingua* was found in two species of fish, the winter and sand flounders, all specimens of these fish were infected. One specimen of *S. aquosus* carried 851 encysted parasites. The infection was heavy enough to cause complete blindness in one eye of this sinistral flatfish.

The halibut was lightly infected, 14% of the fish carrying from 5 to 37 specimens of *C. lingua*. The incidence in the smooth flounder was slightly higher; 21% of the fish harbored 2 to 41 trematodes. The incidence in the

plaice was high, 78% in inshore waters; one fish carried 151 metacercariae. The smooth flounders, captured by ice fishing in Gaspe Bay, were lightly parasitized, while specimens taken offshore carried a greater number of metacercariae and were higher in incidence (63%).

Cryptocotyle lingua, in its adult stage, is mainly a parasite of birds, although it has been found in carnivores and seals. The cercariae develop in *Littorina littorea* (25), the genus *Littorina* is present in the Gulf waters. After passing out from the molluscan intermediate host, they penetrate the second intermediate host, a fish, in this case a species of the Heterosomata. The metacercariae encyst and cause a host reaction; this brings about pigmentation of the area surrounding the parasite.

The preferred site of infection by the metacercariae is either on the dorsal or ventral body surfaces of the flatfish; the tail is also heavily infected dorsally. The parasite is sometimes found on the gill filaments and encysted in the oral cavity.

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CONTRIBUTIONS TO THE KNOWLEDGE OF THE GENUS MELOIDODERA (NEMATODA:TYLENCHIDA), WITH A DESCRIPTION OF M. CHARIS N. SP.[1]

B. E. HOPPER

Abstract

The characters of the genus *Meloidodera* are amended. Additional information on the type species, *M. floridensis*, is presented with a description of the male. A second species, *M. charis*, n. sp., is described, which differs from the type in having a shorter body and smaller stylets, and smaller phasmids in the second-stage larva. Data on host range and distribution are also presented.

The genus *Meloidodera* Chitwood, Hannon, and Esser, 1956 (3), was originally described from Florida attacking the roots of slash pine. Since the genus was erected, other nemas have been found that bear close affinities to the type species. Specimens have been found in California that form cysts and have terminal vulvas, regular body annulations, and larvae with large phasmids.[2] The question arises as to whether these forms belong to this genus. This paper characterizes the genus *Meloidodera* as an aid in identifying specimens and gives an amended description of the genus, a redescription of the type species, *M. floridensis*, including a description of the male, and a description of a second species, *M. charis*, n. sp.[3]

Genus *Meloidodera* Chitwood, Hannon, and Esser, 1956

Description Amended

Heteroderinae. Female body ranging from spheroid to ovoid. Cuticle thickened, with well-developed transverse annulations overlying rows of punctations (Fig. 2). Mature female soft-bodied; cuticle not forming a tough, leathery cyst.

From Chitwood, *et al.*, ". . . faint indications of partial longitudinal grooves posterior to anus and in cervical region, striae interrupted laterally and sometimes fused laterally. Stylet of female quite long with large knobs similar to *Heterodera* or *Criconemoides*".

Eggs retained in body until after first larval molt. Second-stage larva hatching shortly after deposition (ovoviviparity occasionally observed in older specimens). Egg masses not found.

Larvae similar to those of *Heterodera* spp. Phasmids porelike to doughnut-shaped.

[1]Manuscript received June 22, 1960.
Contribution from the Nematology Section, Entomology Research Institute, Research Branch, Canada Department of Agriculture, Ottawa.

[2]Personal communication from Dr. M. W. Allen, Department of Plant Nematology, University of California, Davis, California.

[3]The author wishes to express his appreciation to Dr. Don C. Norton, formerly of the Department of Plant Physiology and Pathology, Texas Agricultural Experiment Station, College Station, Texas, now of the Department of Botany and Plant Pathology, Iowa State College, Ames, Iowa, for contributing the specimens of *M. charis* for this study.

Males (only those of *M. floridensis* known) similar to those of *Heterodera* and *Meloidogyne* spp. but much smaller. Annulated lip region, set off from adjacent narrowed neck region, divisible into labial annule and postlabial annules as in *Meloidogyne* spp. Lateral cheeks not observed. Gonad single, outstretched. Chitwood (personal communication) has observed that the male of *M. floridensis* never goes through a saccate stage like *Heterodera* and *Meloidogyne* spp., but unlike these, is vermiform throughout its life.

Type Species

M. floridensis Chitwood, Hannon, and Esser, 1956.

Differential Diagnosis

Females

The females differ from those of *Meloidogyne* spp. in having a thickened cuticle, a subequatorial vulva, and internal punctations and in not forming either root galls or egg masses.

They differ from those of *Heterodera* spp. in not having a cyst stage and in having well-developed annulations, a subequatorial vulva, and a smaller number of eggs contained in the body.

Males

The males of *M. floridensis* differ from those of *Heterodera* and *Meloidogyne* spp. in their smaller body and shorter spicules (Table I). They also differ from those of both genera in having a constricted neck region directly behind the lip region. This feature causes the spear of *M. floridensis* males to appear

TABLE I

Comparative measurements of males of *Heterodera* and *Meloidogyne* spp. with *Meloidodera floridensis*

	Length (mm)	Spicules (μ)	Spear (μ)
*Heterodera schachtii**	0.8–1.63	33–34.6	28–30
H. humuli	0.85–1.03	32–34.6	27–31
H. punctata	0.9–1.3	34–35	—
H. cacti	1.01	35	—
H. rostochiensis	1.1	34	27–28
H. cruciferae	1.1–1.2	32	25
H. göttingiana	1.21–1.29	32–(44?)	27–(37?)
H. glycines†	1.0–1.4	33.5–36.8	25.5–28.4
Range	0.80–1.63	32–36.8 (44?)	25–31 (37?)
Meloidogyne javanica‡	0.88–1.25	31	20–24
M. hapla	1.0–1.33	29–31	17–21
M. incognita	1.0–2.0	29–36	23–26
M. exigua	1.1	27	17.5–18
M. arenaria	1.27–2.0	31–34	20–24
Range	0.88–2.0	27–36	17–26
Meloidodera floridensis	0.457–0.505	20–22	20–24
Heterodera range	0.80–1.63	32–36.8 (44?)	25–31 (37?)
Meloidogyne range	0.88–2.00	27–36	17–26
Meloidodera floridensis	0.46–0.505	20–22	20–24

*All *Heterodera* data except those on *H. glycines* from Franklin (4).
†From Hirschmann (5).
‡All *Meloidogyne* data from Chitwood (1).

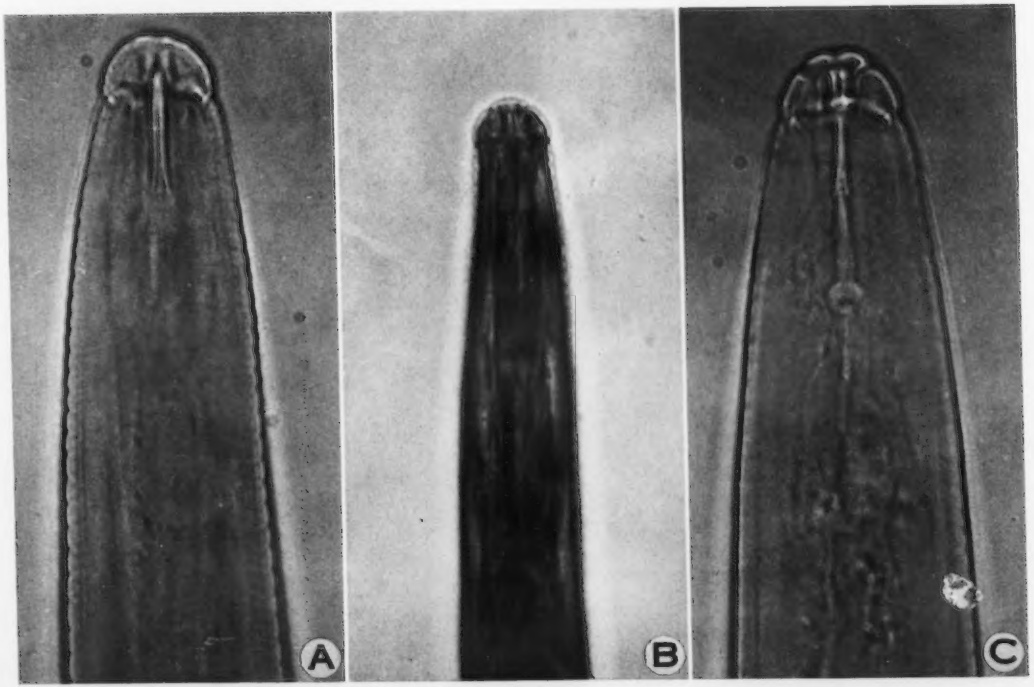
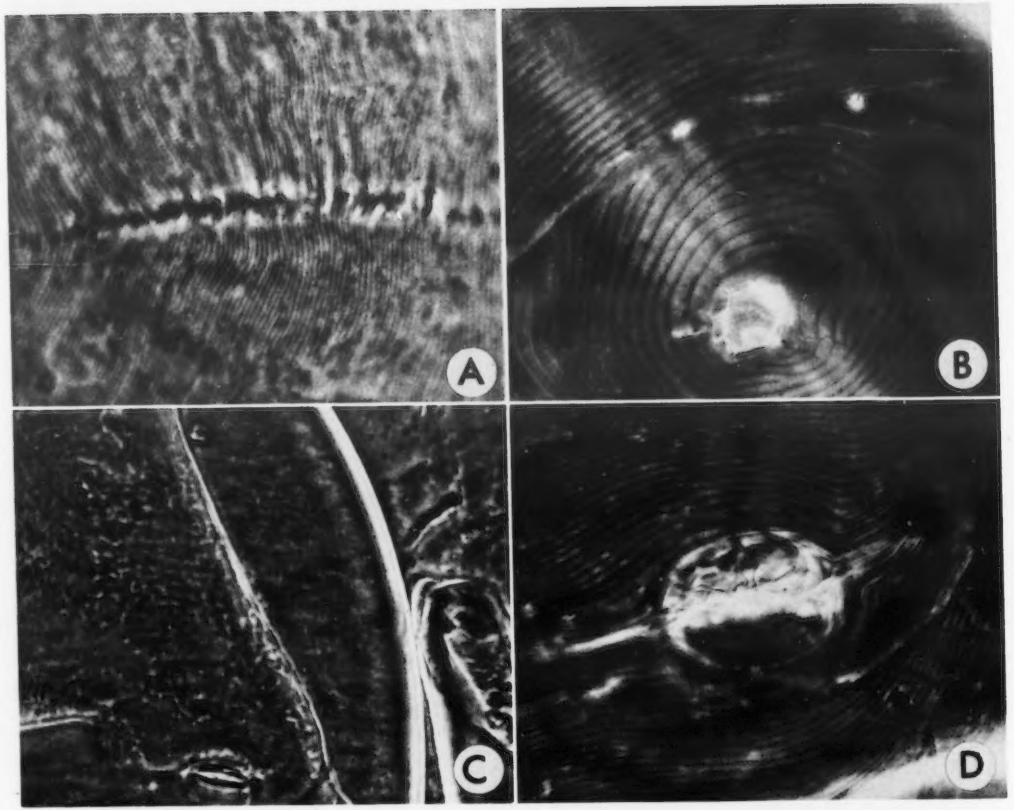


FIG. 1. Male heads. A, *Heterodera* sp.; B, *Meloidodera floridensis*; C, *Meloidogyne hapla*.



Hopper—Can. J. Zool.

much longer in comparison with the neck width, at the level of the stylet knobs, than do those of males of *Heterodera* and *Meloidogyne* spp. (Fig. 1).

They differ from those of *Heterodera* spp. in that the lip region is clearly divisible into a labial annule and postlabial annules. The lip region of *Heterodera* males appears somewhat dome-shaped without any demarcation of the labial annule. In addition to the above characters, males of *Meloidodera floridensis* differ from those of *Meloidogyne* spp. in the absence of lateral cheeks.

Larva

The second-stage larvae can be distinguished from those of *Meloidogyne* spp. by the heavy internal head sclerotization, the larger size of the stylet (24–29 μ against about 10 μ in *Meloidogyne*), and the more pronounced head and body annulations.

The second-stage larvae of *Heterodera* and of *Meloidodera* spp. are extremely similar. No positive separation features were observed that are considered of value at the generic level. The size of the phasmid is of no value as a generic character as the phasmid of *M. charis* is similar to those found in *Heterodera* larvae.

Therefore, for identification to *Meloidodera*, female specimens are essential.

Meloidodera floridensis Chitwood, Hannon, and Esser, 1956

(Figs. 4, A–E; 5, D; 3, A,B,D)

M. floridensis was originally described from the roots of slash pine (*Pinus elliottii* Engelm.) near Olustee, Florida. The presence of males was reported at the time but these were not observed from the type host and consequently were not described. In a subsequent report on pathogenicity trials on slash pine with *M. floridensis*, Chitwood and Esser (2) observed males from this host and reported the ratio of males to larvae obtained by root incubation as about 1:1000.

The males of *M. floridensis* reported in this paper were obtained from roots and soil collected about the roots of slash pine in Alabama, Florida, and Georgia, and are herein described for the first time. Along with the description of the male, the original descriptions of the females and larvae are presented with additional observations.

Males

(Five specimens; Fig. 3, A, B, D.) Small filiform worms, 490 (457–505) μ long and 17.3 (16–19) μ wide. De Man formula: *a*, 28.7 (27.5–30.5); *b*, 3.4 (3.3–3.6);[4] *c*, 196.5 (183–210);[5] *T*, 42.5 (41–44)%.[5] Cuticular annulations approximately 2 μ wide and interrupted laterally by four longitudinal incisures. Lip region 3.3 μ long by 7.4 μ wide and divisible into a rounded labial annule,

[4]Three specimens, measured to base of esophageal glands.
[5]Two specimens.

FIG. 2. *Meloidodera charis*: A, annulations, lateral view; B, annulations in anal region; C, perineal view; D, annulations in vulval region.

which is narrower than the three distinct postlabial annules. Lateral cheeks not observed. Cephalic framework heavily sclerotized. Stylet 20–24 μ long, composed of an anterior part 9.3–13.7 μ long and a posterior part 10.7 μ long. Knobbed portion of stylet 1.6 μ long by 3.3 μ wide, directed somewhat anteriad. Dorsal gland emptying into lumen of esophagus 4–5 μ behind bases of stylet knobs. Esophageal bulb 9–10 μ long by 5.7–7.4 μ wide. Subventral glands extending 70–78 μ posteriorly from base of bulb and overlapping anterior portion of intestine. Nerve ring encircling esophagus a short distance behind esophageal bulb. Excretory pore just behind nerve ring. Neither a hemizonid nor deirids observed.

Spicules 20–22 μ long. Gubernaculum rather small, being 4–5 μ long. Phasmids not observed. Anal body diameter about 10.7 μ. Caudal region of body with the quarter twist characteristic of males in the subfamily Heteroderinae.

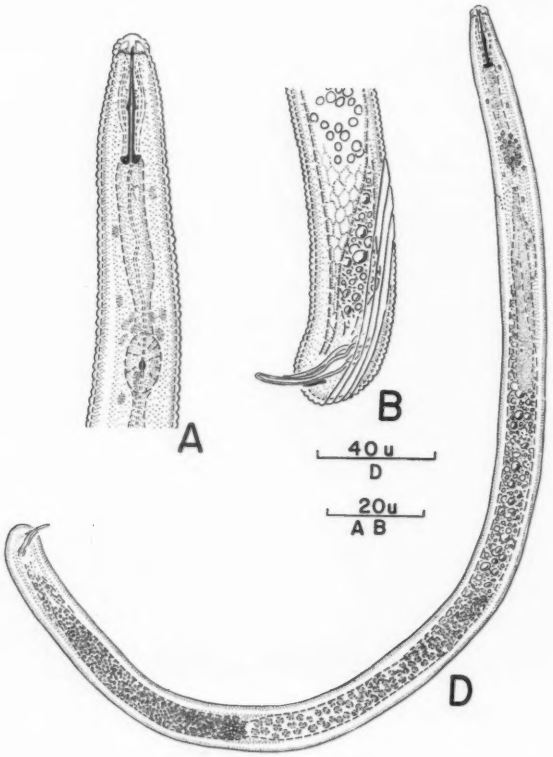


FIG. 3. *Meloidodera floridensis* male: A, anterior end; B, posterior end; D, total view.

Larva

(Fig. 4, A–E.) The original description of the second-stage larva, as presented by Chitwood *et al.*, is given below:

"Larva 500–559 μ long by 19–21 μ wide; *a*, 26–29; *b*, 6.4–7.1; *c*, 8.4–10.0; stylet 27–29 μ long; knobs 2–2.5 μ long by 6–7 μ wide, strongly set off; dorsal gland orifice 4–6 μ posterior to base of stylet . . .; head with 4 annules, 5 μ long by 10–11 μ wide; esophageal glands in ventral column extending 90–95 μ posterior to bulb . . .; excretory pore 108–110 μ posterior to head; lateral fields 5–6 μ wide, sublateral ridges striated at least in the anal region; lateral areas a declivity in this region; phasmids large, circular, 9–12 μ postanal, sometimes appearing as a pore, sometimes as a disc; anal body diameter 15–16 μ; tail elongate, conoid with blunt tip . . .; postprotoplasmic tip 23–35 μ; striae about 2 μ apart."

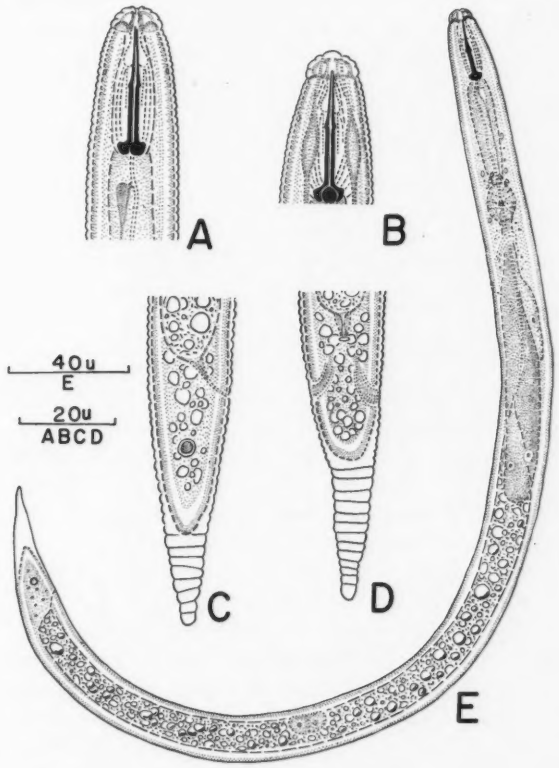


FIG. 4. *Meloidodera floridensis* second-stage larva: A, head, lateral view; B, head, dorsal view; C, tail, lateral view; D, tail, ventral view; E, total view.

In addition, the lengths of all larvae in the present study fell within the range given above, except one specimen that measured 574 μ. The dorsal esophageal gland appears to be distinct from the subventrals and lies in the dorsal sector of the body. This gland extends from the base of the esophageal bulb only about half as far as the subventral glands extend. The subventral glands in living specimens appear to be densely granular, whereas the dorsal gland appears quite clear in comparison.

Female

The original description of the female is given below: "Female 500–800 μ long by 220–400 μ wide; head with 3 clear, probably 4 annules . . .; neck region 120–180 μ long; annules about 1 μ wide in anterior region to about 2 μ wide in body region; stylet 35–37 μ long with knobs 2.5×8 μ; dorsal gland orifice about 5 μ posterior to base of stylet; bulb 35×25 μ; excretory pore near base of neck region, about 130 μ from anterior extremity in specimen with 160 μ neck; vulva on ventral side of body, slightly posterior to middle (450 μ back in specimen 650 μ long); vulva–anus distance, 90–300 μ; anus subterminal, ventral; phasmids 30–40 μ posterior to anus. Eggs varying in size with age of larva up to 115–180 μ long by 55 μ wide. Larva molts once in egg (490 μ long); vitelline membrane present at least in some eggs . . .".

The present study showed that the vulva may protrude in older specimens.

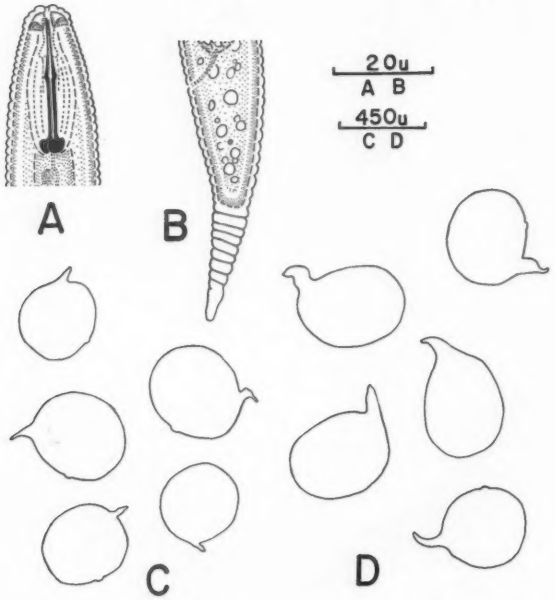


FIG. 5. *Meloidodera charis*, n. sp.: A, anterior portion of second-stage larva; B, tail of second-stage larva; C, adult female body forms. *Meloidodera floridensis*: D, adult female body forms.

Reproduction of *Meloidodera floridensis*

As with the other members of the Heteroderinae, male specimens of *M. floridensis* are found so seldom in comparison with females that the necessity for sexual reproduction is questionable. In all probability parthenogenesis also occurs.

As reported by Chitwood *et al.*, the eggs vary in size according to age; they are 115–180 μ long by 55 μ wide. Oviposition was observed to be continual, the eggs hatching shortly thereafter. The number of eggs contained in 50 dissected females ranged from 42 to 143, with an average of 82 eggs per female. Data on the total productivity of adult females were not obtained.

When *M. floridensis* is in its position on the host, the vulva faces inwardly towards the stele of the root, unlike those of most other sedentary nemas that deposit their progeny at the surface of the root. Thus larvae or eggs, or both, are often observed within root tissues after the adult is gently teased from its position on the root.

Single-celled ova are formed at the germinal end of the ovary and undergo cleavage and increase in size as they pass through the gonad. Initially, the developing eggs are in single file, but at a distance about one-third of the reproductive tract from their origin they become oriented nearly perpendicular to the longitudinal axis of the gonad and are arranged in a double line. Also in this area the embryos develop into first-stage larvae and undergo the first molt. The resulting second-stage larvae may leave the female either enclosed in the eggs or as free larvae.

Meloidodera charis, n. sp.

(Figs. 2, A–D; 5, A–C)

Female

(Figs. 2, A–D; 5, C.) 574 (478–655) μ long by 440 (355–555) μ wide. Lip region apparently consisting of a discoid labial annule and three postlabial annules. Neck region averaging 95 (67–112) μ of the total body length. Thickened cuticle bearing annulations, which are about 1 μ wide in neck region and 2–3 μ wide on rest of body. Annules (usually clear) overlying parallel rows of punctations, but sometimes presenting the vesiculated appearance of some members of the marine family Epsilonematidae.

Stylet 31.7 (30–34.6) μ long, with pronounced knobbed portion 3.3 μ long by 5.0 μ wide. Dorsal gland emptying into lumen of esophagus 3.3–4.0 μ behind bases of stylet knobs. Esophageal bulb 33.3 (31–36) μ long by 31 (29–34) μ wide. Excretory pore near base of neck region. Vulva slightly behind middle of body, protruding in older specimens. Distance between vulva and anus 200 μ in a specimen 533 μ long.

Eggs 120 (111–153) μ long by 41 (37–43) μ wide. One egg in 4-celled stage measuring 110$\times$40 μ, another in 16- or 32-celled stage measuring 116$\times$40 μ, and a third containing a second-stage larva measuring 153$\times$43 μ.

Male

Unknown.

Second-stage Larva

(Fig. 5, A, B.) Larva 460 (406–528) μ long by 19.7 (18–20) μ wide. De Man formula: *a*, 23.0 (20.3–26.4); *b*, 2.7 (2.5–3.0);[6] *c*, 9.9 (8.6–11.5); genital primordium 57.8 (53.7–62.0) %. Cuticle bearing annulations about 1.6 μ wide, interrupted laterally by four longitudinal incisures. Lip region 5 μ long by 10 μ wide and bearing three cross-striations (four annules). Cephalic framework heavily sclerotized. Stylet 24–27 μ long, composed of two portions of which the posterior part is 14.8 μ long. Knobbed portion of stylet 2.5 μ long by 4.9 μ wide and directed somewhat anteriad. Dorsal gland emptying into lumen of esophagus 3–4 μ behind bases of stylet knobs.

Esophageal bulb 10.7–12.3 μ long by 11.5–14.0 μ wide. Esophageal glands arranged as in *M. floridensis*. Subventral esophageal glands extending 146–185 μ posteriorly from cephalic extremity and slightly overlapping anterior portion of intestine. Nerve ring a short distance behind esophageal bulb. Excretory pore 94–109 μ from anterior extremity, just behind nerve ring. Hemizonid directly in front of excretory pore, about three body annules long.

Genital primordium 265 (235–284) μ behind oral opening. Phasmids small, porelike. Tail elongate-conoid, 43–48 μ long, with bluntly rounded terminus.

Differential Diagnosis

Meloidodera, differing from the type and only other species, *M. floridensis*, in that the adult female is comparatively shorter and wider (Fig. 5, C, D) and has a shorter stylet. The stylet knobs and dorsal gland orifice measurements also differ. The larvae differ from those of *M. floridensis* in being slightly shorter, in having a shorter stylet with a longer stylet extension, and in having small phasmids.

Type Host

Honey mesquite, *Prosopis juliflora* (Sw.) D.C. var. *glandulosa* (Torr.) Cockerell.

Type Locality

Greenhouse, Texas Agricultural Experiment Station, College Station, Texas.

Type

Canadian National Collection of Nematodes, No. 1821.

Paratypes

Canadian National Collection of Nematodes, No. 1821*a*.

Distribution and Host Range of *Meloidodera* spp.

M. floridensis has been taken from soil and root samples collected near Auburn and Mobile, Alabama; Cantonment, Day, Gainesville, Munson, and Olustee, Florida; Sandersonville and Townsend, Georgia; Harrisville,

[6]Measured to base of esophageal glands.

New Jersey; and Clayton, North Carolina. In a report on nemas in forest nurseries, Hopper (7) recorded finding *M. floridensis* on roots of sand pine (*Pinus clausa*), Australian pine (*P. nigra*), longleaf pine (*P. palustris*), and loblolly pine (*P. taeda*), in addition to the type host. Hutchinson and Reed (8) have subsequently recorded pitch pine (*Pinus rigida*) and shortleaf pine (*P. echinata*) as hosts of this nema. Also, a single female of *M. floridensis* was taken from roots of an oak seedling (*Quercus* sp.) collected in Auburn, Alabama.

Meloidodera charis n. sp. has been found only in its type locality. Although Norton (9) found *Meloidodera* spp. in various regions of Texas, species determinations were not reported. In Texas, *Meloidodera* spp. have been collected from the following land resources areas: East Texas Timberlands, Coast Prairie, Black Land Prairies, Rolling Plains, and Trans-Pecos. *Meloidodera* spp. were associated occasionally with St. Augustine grass.

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NEMATODE PARASITES FROM TURKISH VERTEBRATES

AN ANNOTATED LIST[1]

G. A. SCHAD, R. E. KUNTZ, AND W. H. WELLS

Abstract

An annotated list of nematodes recovered from 35 species of Turkish vertebrates is presented. In addition to information enabling improved taxonomic characterization of several species, the annotations describe *Heligmosomum* sp., a parasite of *Crocidura russula*, and discuss the value of the dorsal ray in distinguishing between species of the Heligmosomidae. Observations are made on the parasitic stages in the life history of *Angusticaecum holopterum* and their distribution in the host. Notes are given on the recognition of the genus *Pseudophysaloptera*, and the male of *Rictularia proni* is described.

The nematodes recorded in this paper were collected in Turkey during August 1953 and July 1954 and forwarded to the Institute of Parasitology for identification. This study is based on 167 collections from 35 host species. All the nematodes identified are listed below but only those requiring description or comment appear in the annotations.

List of Nematodes Recovered[2]

Parasite	Host	No. examined	No. parasitized
Rhabdias sp.	*Rana macrocnemis*	13	1
Rhabdias sp.	*Bufo viridis*	10	7
Entomelas dujardini (1)	*Anguis fragilis*	9	6
Entomelas entomelas	*Anguis fragilis*	9	1
Oswaldocruzia skrjabini	*Anguis fragilis*	9	7
Oswaldocruzia skrjabini	*Lacerta viridis*	2	1
Oswaldocruzia skrjabini	*Lacerta taurica*	1	1
Oswaldocruzia filiformis	*Bufo regularis*	4	3
Oswaldocruzia filiformis	*Rana macrocnemis*	13	7
Oswaldocruzia sp. (females only)	*Bufo viridis*	10	2
Molinostrongylus ornatus	*Plecotus auritus*	6	4
Molinostrongylus ornatus	*Miniopterus schreibersi*	9	8
Molinostrongylus alatus	*Myotis m. myotis*	6	2
Strongylocantha glycirrhiza	*Rhinolophus ferrum-equinum*	2	2
Heligmosomum sp. (2*a*)	*Crocidura russula*	4	2
Heligmosomum azerbaidjani (2*b*)	*Apodemus sylvaticus tauricus*	13	5
Heligmosomum sp. (females only)	*Arvicola terrestris hintoni*	2	1
Heligmosomum costellatum (2*b*)	*Microtus g. guentheri*	2	1

[1]Manuscript received April 18, 1960.

Contribution from the Institute of Parasitology, McGill University, Macdonald College P.O., Que., Canada, with financial assistance from the National Research Council of Canada. The parasites upon which this paper is based consist of two collections taken by Dr. Robert E. Kuntz, CDR, MSC, USN, and LCDR William H. Wells, MSC, USN (U.S. Naval Medical Research Unit No. 2, Taipei, Taiwan). The first collection was taken as part of the activities of the U.S. Naval Medical Reconnaissance Group to Turkey in 1953. B. H. Randall HMI, U. S. Navy, gave technical assistance and Dr. Edip Beker, representative of the Turkish Ministry of Health, gave general assistance and served as the group's liaison. The second collection (Wells) was taken when a similar group returned to eastern Turkey to continue field studies in 1954. Dr. Harry Hoogstraal, Head, Department of Medical Zoology, NAMRU-3, Cairo, Egypt, gave assistance in collection of animals examined and has provided identifications for the mammalian hosts. Dr. Austin K. Rand, Curator of Birds, Chicago Natural History Museum, has provided identifications for the birds, and Dr. Robert F. Inger, Curator of Reptiles, same institution, has provided identifications for the reptiles and amphibians. Dr. Roy C. Anderson, Ontario Research Foundation, identified the nematode *Skrjabinelazia taurica*.

[2]A number in parentheses following the name of a parasite refers to the relevant annotation.

Parasite	Host	No. Examined	No. parasitized
Crenosoma striatum (3)	*Erinaceus europaeus concolor*	8	5
Aspicularis tetraptera	*Mus m. musculus*	3	2
Syphacia sp. (females only) (4)	*Apodemus sylvaticus tauricus*	13	6
Syphacia sp. (females only) (4)	*Mus m. musculus*	3	2
Syphacia sp. (females only) (4)	*Meriones blackleri intraponticus*	1	1
Tachygonetria conica (5)	*Testudo graeca ibera*	8	6
Tachygonetria dentata (5)	*Testudo graeca ibera*	8	3
Tachygonetria longicollis (5)	*Testudo graeca ibera*	8	6
Tachygonetria macrolaimus (5)	*Testudo graeca ibera*	8	6
Tachygonetria microstoma (5)	*Testudo graeca ibera*	8	3
Tachygonetria robusta (5)	*Testudo graeca ibera*	8	3
Tachygonetria stylosa (5)	*Testudo graeca ibera*	8	2
Tachygonetria thapari (5)	*Testudo graeca ibera*	8	5
Tachygonetria uncinata (5)	*Testudo graeca ibera*	8	4
Tachygonetria vivipara (5)	*Testudo graeca ibera*	8	1
Atractis dactyluris	*Testudo graeca ibera*	8	6
Cosmocerca ornata (6)	*Rana macrocnemis*	13	8
Cosmocerca ornata	*Rana ridibunda*	31	23
Cosmocerca ornata	*Bufo viridis*	10	1
Cosmocerca commutata	*Bufo viridis*	10	4
Aplectana schneideri (7)	*Bufo regularis*	4	4
Aplectana brumpti	*Bufo viridis*	10	3
Aplectana brumpti	*Pelobates syriacus*	1	1
Oxysomatium brevicaudatum	*Bufo regularis*	4	3
Oxysomatium brevicaudatum	*Bufo viridis*	10	1
Oxysomatium brevicaudatum	*Rana macrocnemis*	13	2
Oxysomatium brevicaudatum	*Rana ridibunda*	31	1
Oxysomatium brevicaudatum	*Anguis fragilis*	9	1
Oxysomatium brevicaudatum	*Natrix natrix*	1	1
Falcaustra lambdiensis	*Clemmys caspica rivulata*	8	5
Falcaustra lambdiensis	*Emys orbicularis*	2	2
Toxocara mystax	*Felis domestica*	9	9
Toxocara canis	*Vulpes vulpes*	3	1
Toxascaris leonina	*Vulpes vulpes*	3	1
Angusticaecum holopterum (8)	*Testudo graeca ibera*	8	8
Porrocaecum sp. (females only)	*Corvus monedula soemmeringii*	1	1
Porrocaecum sp. (larvae)	*Erinaceus europaeus concolor*	8	2
Porrocaecum semiteres	*Vanellus vanellus*	1	1
Contracaecum nehli	*Gallinula c. chloropus*	1	1
Contracaecum sp. (larvae)	*Falco s. subbuteo*	1	1
Contracaecum (larvae)	*Actitis hypoleucos*	1	1
Skrjabinelazia taurica	*Lacerta taurica*	1	1
Skrjabinelazia taurica	*Lacerta viridis*	2	1
Camallanus microcephalus (9)	*Clemmys caspica rivulata*	8	2
Camallanus microcephalus	*Emys orbicularis*	2	2
Rictularia amurensis (10)	*Dryomys nitedula*	1	1
Rictularia proni (10)	*Apodemus sylvaticus tauricus*	13	2
Rictularia cahirensis	*Vulpes vulpes*	3	1
Hedruris androphora (11)	*Triturus cristatus*	15	14
Hedruris sp. (females only)	Unidentified trout	1	1
Hedruris sp. (females only)	*Natrix natrix*	1	1
Spiroxys contortus (12)	*Clemmys caspica rivulata*	8	1
Spiroxys contortus	*Emys orbicularis*	2	2
Spiroxys contortus (larvae)	*Triturus cristatus*	15	5
Physaloptera clausa (13)	*Erinaceus europaeus concolor*	8	8
Physaloptera sp. *s.l.* (larva)	*Lacerta viridis*	2	1
Physaloptera alata (14)	*Falco tinninculus*	2	1
Pseudophysaloptera soricina (15)	*Crocidura russula*	4	1
Desmidocerca sp. (immature)	*Coracius g. garrulus*	2	1
Desmidocerca sp.	*Athene noctua*	1	1
Litomosa chiropterorum	*Plecotus auritus*	6	3
Litomosa chiropterorum	*Miniopterus schreibersi*	9	7
Litomosa sp. (females only)	*Myotis m. myotis*	6	1
Capillaria sp.	*Corvus monedulus soemmeringii*	1	1
Trichuris muris	*Apodemus sylvaticus tauricus*	13	2

Annotations

1. Entomelas dujardini (Maupas, 1916) Travassos, 1930

As far as is known to the authors, the latest description of this species is that of Travassos (23). A discrepancy between his measurements and ours is found in the distance from the anterior end at which the nerve ring is located. In specimens similar in length to those reported by Travassos (that is, 4.5 to 6.5 mm) the nerve ring is situated twice as far posteriorly (0.28 to 0.31 mm vs. 0.15 mm).

2(a). Heligmosomum sp. (Figs. 1–7)

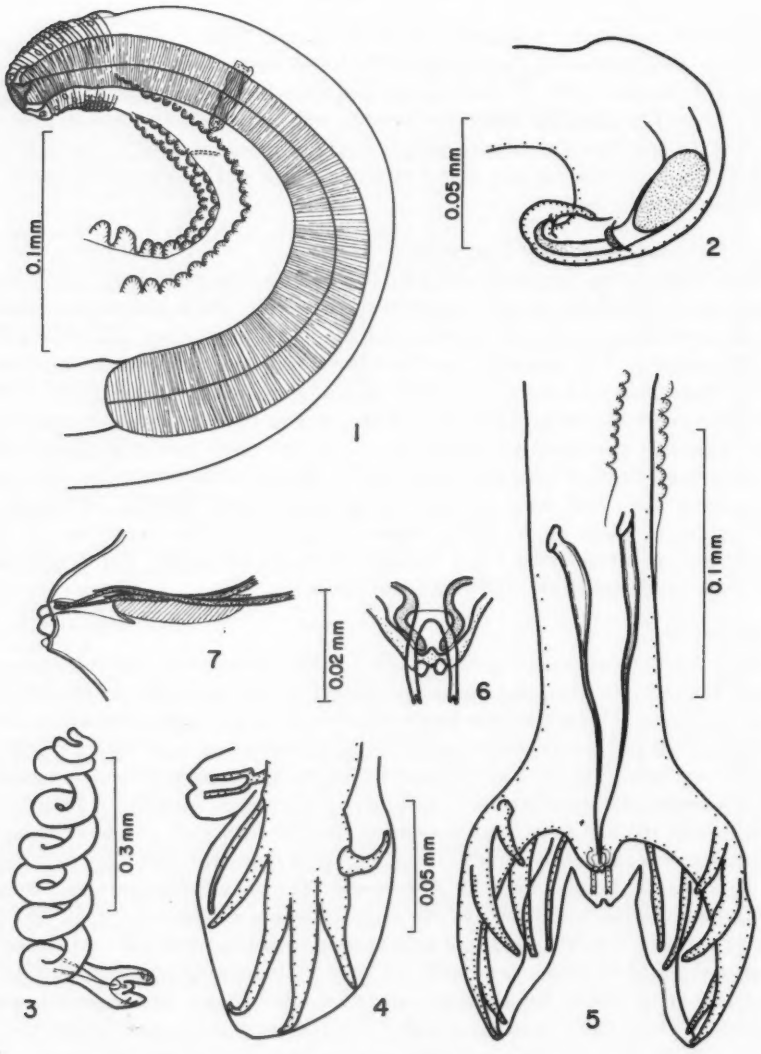
Two males, two females, and two fragmentary females from the small intestine of *Crocidura russula* comprise the material. These specimens cannot be assigned to any presently named and adequately described species known to the authors. The material may be *Strongylus depressus* Dujardin, 1845, since redescribed as *Longistriata depressa*, but the authors are doubtful if the organism currently recognized as *L. depressa* is in fact the same organism as that originally described by Dujardin (5). If the more recent workers have actually been dealing with the same form as described by Dujardin then the nematodes described here probably represent a new species. A detailed description is given to facilitate future recognition. The condition of the specimens permitted only a few measurements to be taken. The specimens are to be deposited in the U.S. National Museum.

Description

Both sexes minute and greatly coiled. Male about 1.6 mm and female about 1.82 to 1.86 mm long. Better preserved of two males wound spirally to form cylinder. Three striated longitudinal cuticular ridges extending posteriorly from behind cephalic inflation and terminating near anterior end of spicules in male (Fig. 5) and at about 0.31 mm from posterior end in female. Ridges confined to surface forming inner face of each winding of body and forced into regular folds and appearing deeply scalloped. Cephalic cuticle inflated and prominently striated (Fig. 1). Head diameter, including inflation, 22 to 28 μ in female and 21 μ in male. Bead-like ornamentation under cuticular inflation and between the striae in some specimens. Small mouth cavity present, 6 to 8 μ by 2 to 3 μ in female. Oesophagus 0.254 to 0.262 mm long and 0.032 to 0.035 mm wide at base in female, with nerve ring surrounding it at about its anterior third. Excretory pore not observed with certainty. Duct-like structure, possibly the excretory duct, seen in one specimen at level of nerve ring but obscured by the longitudinal ridges of body (Fig. 1).

Male

Bursa symmetrical with two well-developed lateral lobes and small notched dorsal lobe (Figs. 4–5). Broad common trunks give rise to all rays except the dorsals. Ventroventral ray relatively small, originating near base of common trunk and curving anteriorly. Lateroventral ray diverging widely from



FIGS. 1–7. *Heligmosomum* sp. from *Crocidura russula*
1. Anterior end of female.
2. Posterior end of female.
3. Male (entire).
4. Lateral lobe of bursa (lateral).
5. Posterior end of male (ventral).
6. Dorsal ray, accessory ray, and genital cone (dorsal).
7. Genital cone, spicule tips, and gubernaculum (lateral).

ventroventral, grouped with lateral rays and extending posteriorly with them. Anterolateral and mediolateral rays similar, associated closely at base, diverging distally and extending posteriorly. Posterolateral ray inserted more anteriorly, more divergent, and more dorsally directed. Externodorsal rays separate in origin from dorsal ray; they extend into lateral lobes, ending near tip of dorsolateral rays. Dorsal ray, consisting of stem with two distally bifurcated branches, extends into small median lobe of bursa.

Lying between dorsal ray and genital cone is small accessory membrane supported by minute accessory ray consisting of broad common trunk and two branches (Fig. 6). Branches widely spaced at origin converge distally. Membranous flap incised between convergent tips of accessory ray.

Genital cone bears paired large and small papillae at either side of cloacal aperture (Figs. 6–7). Spicules, 0.13 mm long, give over-all impression of consisting of three parts, expanded proximal end followed by thin middle portion followed, in turn, by still thinner distal tip (Fig. 5). Actually, midsection of each spicule consists of two parts extending posteriorly in parallel; near the tip one part ends while other forms now thinner distal end of spicule (Fig. 7). Extreme tip slightly spatulate. Gubernaculum present.

Female

Posterior region tightly coiled. Anus and vulva near posterior end (Fig. 2). Body expanded immediately anterior to vulva. Beginning at vulva body tapers rapidly to anus and ends in a much more slender conical tail tipped by a spine. Eggs oval, thin-walled, 47 to 51 μ by 28 to 29 μ.

Discussion

Skrjabin, Shikhobalova, and Shul'ts (18) list no species of *Heligmosomum* from shrews. (*Strongylus depressus* is included in the genus *Longistriata*.) Although our material cannot be identified with any species of *Heligmosomum* listed and described, it does show some resemblance to a number of species known from rodents. These include *H. juvenum* Kirschenblatt, 1949, *H. travassosi* (Shul'ts, 1926), *H. turgidum* (Walton, 1923), and *H. yorkei* (Shul'ts, 1926). However, our *Heligmosomum* sp. differs from all of these in being a much smaller species with much shorter spicules. Of the species listed, *H. juvenum* has the shortest spicules and these are almost four times as long as those of our specimens. It also differs from all of these in various details, that is, from *H. juvenum* in the structure of the cuticular ridges, from *H. turgidum* in the presence of an accessory ray, and from *H. yorkei* in having an elongate bursa with normal rays rather than a short bursa with very short stout rays.

In *Longistriata depressa*, as redescribed by Thomas (20) the male is straight, while Dujardin (5) described it as strongly wound in spiral turns. Our material agrees with Dujardin's description in this respect. Dujardin also describes four longitudinal striated cuticular ridges per side that are stiff and prohibit unrolling of the worm without twisting. Thomas reports an unspecified number of indistinct ridges while we find three prominent, striated, deeply scalloped ridges unilateral in distribution. Both previous authors give a

spicule length about twice as long as found in our material and neither describes the accessory structures we observed in the bursa, but these are easily overlooked.

Travassos (22) suggested that the longitudinal ridges as described by Dujardin were fixation artifacts. This opinion may have influenced subsequent authors to ignore the ridges and degree of spiral coiling in assigning nematodes to Dujardin's species. However, Dujardin states that his description was based on two collections of numerous specimens and thus it is doubtful whether he was misled by fixation artifacts.

The differences between *L. depressa* sensu Thomas and the original description by Dujardin are clear from the previous discussion. Our material is in greater agreement with Dujardin's description in several respects but the difference in spicule measurements and the unilateral, rather than bilateral, distribution of the longitudinal ridges prevents us from assigning our specimen to *S. depressus* Dujardin.

2(b). Heligmosomum spp.

The study of *Heligmosomum* sp. (described above), *H. azerbaidjani*, and *H. costellatum* together with other material not listed, and the critical evaluation of the literature in the course of this work, indicated that the dorsal ray in many Heligmosomidae may well be a structure degenerating in the course of evolution. We suggest, therefore, that the use of this character for taxonomic purposes may prove to have been very misleading. The dorsal ray in many Heligmosomidae appears to be a vestigial structure, its function presumably taken over by a new structure, the accessory ray, which occurs frequently in this group. Where rudimentation has been studied in detail it has been shown that these structures are highly variable; in some cave-dwelling fishes, for example, a structure as complex as the eye can vary from absence to functional presence (3, pp. 283–285; 15, pp. 236–240). Vestigial structures, that is, organs being reduced in the course of evolution are without adaptive value and thus may vary markedly without disadvantage to the organism. Selection for a genotype determining the precise duplication of these structures is weak, and thus such characters may vary widely. Helminthologists may have built a classification for the Heligmosomidae on a character the value of which for taxonomic purposes is seriously questionable on theoretical grounds.

In practice, the widespread use of differences in dorsal ray pattern indicates that helminthologists have found this character useful. This, however, does not validate the practice. Variation studies are still practically unknown in helminth parasite taxonomy and thus the theoretically predicted variation of the dorsal ray in heligmosomids can remain generally unrecognized, variants in this character being simply described as valid species. We have, therefore, avoided comparisons of species on the basis of this structure although such comparisons have constituted the main argument for distinguishing between species of heligmosomids in much previous work.

3. Crenosoma striatum (Zeder, 1800) Molin, 1861

Variations from the measurements given by Dougherty (4) for this species are: in males about 6 mm long, with spicules averaging 280 μ long, the gubernaculum measures 89 μ, the oesophagus only 260 to 290 μ. In females, 10 to 14 mm, the tail is only 120 to 140 μ long.

4. Syphacia spp.

Syphacia is recorded from three hosts. Until Roman (16) and others and, more recently, Stammer (19) showed that several sibling species exist that are remarkably host specific, it was generally considered that all specimens from two of these hosts belonged to *Syphacia obvelata.*

On the basis of host distribution and location within the host (according to Roman and Stammer) our material should be assigned as follows:

Specimens from the large intestine of *Mus musculus* to *Syphacia obvelata.*

Specimens from the small intestine of *Apodemus sylvaticus tauricus* to *Syphacia stroma.*

Specimens from the large intestine of *A. s. tauricus* to *Syphacia frederici.*

Unfortunately, we have only female specimens most of which are in poor condition and, without morphological support, we can do no more than list all of them as *Syphacia* spp.

5. Tachygonetria spp.

Ten species of this genus were identified, as listed, from *Testuda graeca ibera.* This material, of considerable general systematic interest, has been given especially detailed study and the results will be published separately.

6. Cosmocerca ornata (Dujardin, 1845) Railliet and Henry, 1916

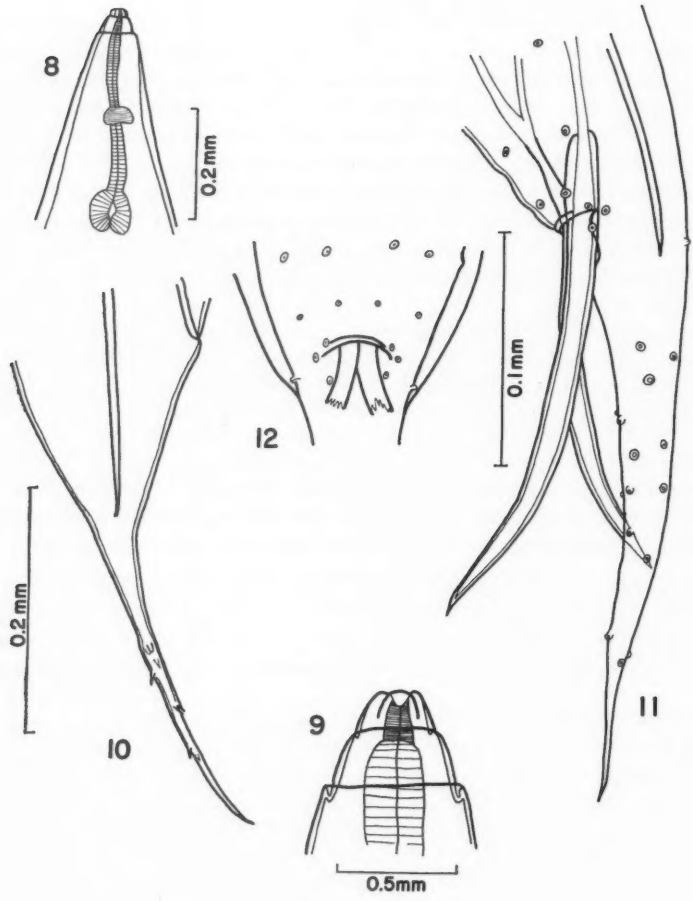
The female tail filament is long and the oesophagus short, as in Fig. 6 by Travassos (24), and Plate 116 of Lopez-Neyra (9), not like Travassos' Fig. 5, nor with an elongate anterior oesophageal section as in Travassos' Fig. 7.

7. Aplectana schneideri Travassos, 1931 (Figs. 8–12)

This nematode is inadequately illustrated in the literature and we therefore present Figs. 8–12. Figure 12 shows a ventral view of the male tail with two pairs of the postanal papillae, the two pairs of adanal papillae, and eight of the preanal papillae. These eight papillae represent the last two papillae in each of four longitudinal rows that extend anteriorly as far as the excretory pore. The four papillae composing the transverse rows shown may be interpreted as two pairs, that is, a sublateral pair and a subventral pair, and their respective longitudinal series the sublateral rows and the subventral rows. The papillae of these subventral rows while usually paired sometimes occur singly and occasionally in threes.

8. Angusticaecum holopterum (Rud., 1819) Baylis, 1920 (Table I)

Larvae and (or) adults were found in all eight *Testudo graeca ibera* examined, the larvae usually in the lungs and the adults in the intestine. Dubinina (in Mozgovoi (11)) suggested that the larvae migrate through the definitive host before becoming mature in the intestine. Our data, as shown in Table I,



FIGS. 8–12. *Aplectana schneideri*
8. Anterior end (female).
9. Same enlarged.
10. Tail of female.
11. Tail of male (lateral).
12. Tail of male (ventral).

TABLE I

Differential distribution of larval vs. adult *A. holopterum* in *Testuda graeca ibera*

	Gut		Body cavity		Lungs		Total	
Host No.	Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
1	23	1*	0	0	0	70	23	71
2	16	0	0	0	0	0	16	0
3	21	0	14	30	0	0	35	30
4	6	2	0	0	0	181	6	183
5	11	0	0	0	0	0	11	0
6	6	0	0	0	0	0	6	0
7	1	0	0	0	0	0	1	0
8	1	0	0	0	0	2	1	2
Total	85‡	3	14	30	0	253	99†	286

*In molt to adult stage.
†Fifty one males and 48 females.
‡Fifteen in stomach, 42 small intestine, 28 large intestine.

support this suggestion. Of 386 larvae recovered only 3 were found in the intestine, 30 in the body cavity, and 253 in the lungs. On the other hand, of 101 adults only 14 occurred outside the stomach and intestine.

It is interesting to note that *A. holopterum* larvae have prominent interlabia whereas these structures are absent in the adult. There is no question here of possible confusion of two species—the larva of one species and the adult of another—because a larva was found in process of molting into the adult stage and the interlabia may be seen on the larval head but not on that of the adult.

9. Camallanus microcephalus (Dujardin, 1845) Railliet and Henry, 1915

Our collections, which fit the recent description of this parasite by Lopez-Neyra (9) very well, show some variation in the number of caudal papillae in the male. Seven preanal papillae were found in all specimens examined whereas adanal papillae occurred in from two to four pairs, and postanal papillae in three to four pairs.

10. Rictularia spp. (Table II, Fig. 13)

One female *Rictularia amurensis* is reported from *Dryomys*, while a male and female *R. proni* are reported from *Apodemus*. However, it was with some hesitation that we chose to divide the specimens between two species because the worms show considerable similarity.

As presently defined, *R. amurensis* and *R. proni* differ, respectively, as follows:

(*a*) 50 vs. 44 cuticular combs,
(*b*) 52 vs. 28–32 denticles, and
(*c*) rounded vs. pointed denticles on the anterior lip.

Table II shows that our two female specimens each fit one of these species very well insofar as the number of cuticular processes and the number of denticles are concerned. However, in both specimens, the denticles are apically rounded, that is, knob-like.

TABLE II

Comparative measurements and counts of *Rictularia* spp. Measurements in millimeters

	Female from *Dryomys*	*Rictularia amurensis*	Female from *Apodemus*	*R. proni* sensu Dollfus and Desportes, 1944
Total length	24	51–60	44	48–50
No. of denticles	50	52	32	28–32
Oesophagus, length	3.6	5.2	3.7	4.7
Cervical papillae from anterior end	0.63	0.82	0.52	0.78–0.82
Total number of combs and spines	49	50	44	44
Prevulvar	30	33	33	32–34
Postvulvar	19	17	11	10–12
Egg	50×33–34 μ	48×33 μ	—	50×30 μ

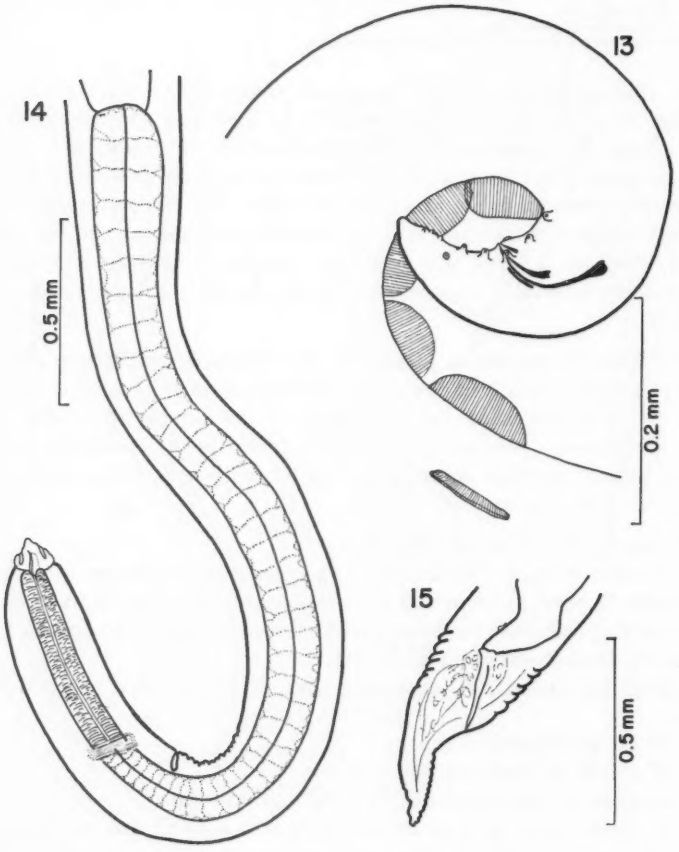


FIG. 13. *Rictularia proni*, tail of male.
14. *Spiroxys* larva, anterior end (lateral).
15. *Spiroxys* larva, posterior end (lateral).

We suspect that, in time, *R. amurensis* and *R. proni* will be shown to be synonyms. Gibbs (6) has studied variability in *R. cahirensis* and shown that three previously recognized species were synonymous. If the degree of variability demonstrated by Gibbs is valid throughout the genus then certainly *R. amurensis* and *R. proni* will be among the first to be synonymized. However, Tiner (10), who has had considerable experience with the genus has continually held to a quite narrow concept of a species in this genus.

We have elected to follow the safest course, that is, to identify the material as representing both *R. amurensis* and *R. proni*. If these species are shown to be synonymous these records can easily be merged.

The male *R. proni* has not been described. Therefore, we present Fig. 13 and the following data.

Length 3.95 mm with 39 combs extending from just behind mouth to anterior caudal fan. Fans five in number. Mouth opens dorsally, filled with debris, thus dentition not seen. Cephalic papillae as previously described for female. Oesophagus 0.90 mm long, of which muscular sector is 0.23 mm long. Nerve ring surrounds oesophagus at 0.19 mm from anterior end. Excretory pore at level of sixth comb, 0.31 mm from anterior end, followed by cervical papillae 0.37 mm from anterior end. Spicules 53 and 105 μ, the longer having a proximal bulb. Gubernaculum present. Additional chitinoid formations visible near cloacal opening. Two pairs large subventral papillae anterior to anus accompanied by single mid-ventral papilla on anterior lip of cloaca. One pair subventral adanal papillae and two pairs large subventral postanal papillae followed by pair of lateral papillae which, in turn, are followed by three pairs small papillae along ventral side of tail near its tip.

A comparison of our description of the male *R. proni* with descriptions of *R. citelli* (= *R. halli*) (17, 21) will show that these are remarkably similar. This seems to us a further indication that many *Rictularia* of rodents, with 35 to 50 cuticular processes in the female and with dorsally directed mouths, may be synonyms.

11. Hedruris androphora Nitzsch, 1821

This parasite was found in 14 of 15 newts, *Tritrurus cristatus*, from Lake Abant. In addition, *Hedruris* females were found in an unidentified trout, and in one *Natrix natrix* from the same area. The two females from the trout are identical with those found in the newts and are probably *H. androphora*. The single female from *N. natrix*, while probably also *H. androphora*, contained eggs differing from those of the other specimens in that they lacked the usual lateral thickenings.

H. androphora is normally a parasite of amphibians (but Baylis (1) recorded *Hedruris spinigera* from trout in New Zealand, where trout are not native). The trout may become infected by eating newts or other amphibians infected with the parasite, and *Natrix natrix* probably receives its infection (or pseudo-infection) from the same source.

12. Spiroxys contortus (Rudolphi, 1819) Schneider, 1866 (Figs. 14–15)

Adults and advanced larvae were found in several turtles from Lake Emir and in one from Sapanca. Younger larvae, almost certainly *Spiroxys* and probably *S. contortus*, were found in newts (*T. cristatus*) from Lake Abant (Figs. 14–15) (7).

Our collections show a range of measurements in some structures exceeding that given by Hedrick (7): spicules up to 4.5 mm, gubernaculum 0.37 to 0.40 mm long, and tail 0.60 to 0.65 mm long.

13. Physaloptera clausa Rudolphi, 1819 (Figs. 16–18)

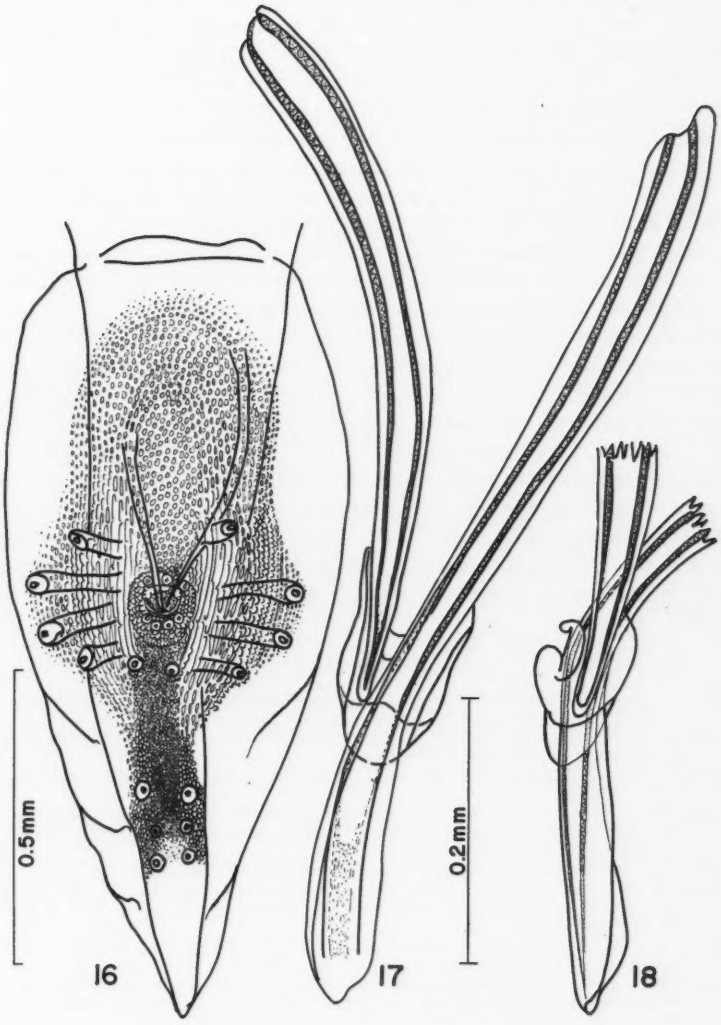
Since Ortlepp (12) redescribed this species on the basis of type and additional material from European hedgehogs it has been clearly recognizable, and the confusion surrounding the synonymy of *P. dispar* von Linstow, 1904 and "*P. clausa*" of Seurat, 1917 with *P. clausa* Rudolphi, 1819 is clarified. Baylis (2) and Ortlepp (13) agree that *P. dispar* von Linstow is a separate and valid species parasitizing African hedgehogs. Isaichikov (8) described *P. seurati* and *P. clausa orientalis* from hedgehogs but unfortunately his paper is not available to us and we know of no other account of his subspecies.[3] Our material shows some minor differences from *P. clausa* as redescribed by Ortlepp and it might be referable to *P. clausa orientalis*, because presumably Isaichikov erected his subspecies on the basis of small differences from the concept of *P. clausa* conveyed by the literature. It is in the male tail and spicules (Figs. 16–18) that differences occur between our specimens and Ortlepp's description. A gubernaculum (not mentioned by Ortlepp) is present. The left spicule at low magnifications and in most whole mounts appears to be pointed (Fig. 16) but at higher magnifications, in exceptional whole mounts, and after dissection, is seen to be spatulate (Figs. 17–18). It should be noted that Ortlepp's (14) description was based on whole mounts and thus the gubernaculum and details of the spicule tip could easily have gone undetected.

14. Physaloptera alata Rudolphi, 1819

P. alata, of several authors, is obviously heterogeneous. Forms described under this name fall into two groups which are probably two species. The first group is represented by *P. alata* of Seurat, 1914 and its various varieties proposed by the same author. In these the vulva is situated anteriorly, that is, close to the end of the oesophagus. In the second group, the vulva is nearer mid-body and includes *P. alata* Schneider, 1866, *P. alata* Ortlepp, 1922, and *P. galinieri* Seurat, 1914, which Ortlepp (12) considered a possible synonym of *P. alata*.

We follow Lopez-Neyra (9) in considering the name *P. alata* to be restricted to the first group, and assign our specimens to it since the vulva is situated anterior to the end of the oesophagus and the spicules are slender and equal, measuring about 0.5 mm in length.

[3]This paper is apparently unavailable in both the United Kingdom and the United States. The copy listed in the Index Catalogue of Medical and Veterinary Zoology could not be located.



FIGS. 16–18. *Physaloptera clausa*
16. Male tail (ventral).
17. Spicules and gubernaculum (ventral).
18. Spicule tips and gubernaculum (lateral).

15. Pseudophysaloptera soricina Baylis, 1934

Pseudophysaloptera is recognized as a genus distinct from *Physaloptera* on the basis of the absence of stalked pericloacal papillae in the male of the former and their presence in the latter. In addition, in *Pseudophysaloptera* there is a characteristic large saddle-shaped depression surrounding the vulva in all females. The genus is known only from shrews.

However, in the authors' specimens it has been observed that the external apical labial tooth is absent in all specimens. This character is not clearly described in the literature but one is left with the impression that the lack of the external apical tooth holds for all *Pseudophysaloptera*. If this is true, then absence of the external tooth would be a better characteristic than the lack of pedunculated pericloacal papillae in the male for recognition of *Pseudophysaloptera* as distinct from *Physaloptera*.

In the specimens at hand (seven males and seven females), stalked papillae occur in some individuals, but never are all four pairs of stalked papillae, as occur in *Physaloptera*, visible. Instead, one or two papillae, at random, can be seen extending into the alae from the body of the tail, and even these are greatly reduced in comparison with the form typical of *Physaloptera*. These vestiges, often appearing to be reduced to naked nerves, are seen only with difficulty at high magnification, and overclearing must be avoided.

Physaloptera kotlani Kobulej links *Pseudophysaloptera* to *Physaloptera*, sensu strictu. This form has been described as having an external apical tooth and a full complement of stalked papillae although these are much reduced.

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OBSERVATIONS ON THE RETINA OF FLORIDA CHAMELEON (ANOLIS CAROLINENSIS)[1]

M. A. ALI[2]

Abstract

The structure of the *A. carolinensis* retina is similar to that of diurnal lacertilians described in the literature. It possesses 10 layers. The visual cell layer is made up of single and double cones. No rods are present. The internal nuclear layer is thicker than the external nuclear layer. The nuclei and ganglion cells of light- and dark-adapted animals do not show any differences in staining. A prominent conus papillaris and a fovea are present. The epithelial pigment layer and the cones do not undergo any photomechanical changes. It was not possible to condition the chameleons to yield any behavioral responses.

Introduction

In view of the phylogenetic relationship between the reptiles and the other two classes of amniotes, it was felt that an understanding of their visual process, especially their ability or the lack of it, to differentiate among various wave lengths, would help to elucidate the evolutionary significance of color vision among the members of these three classes.

Color vision in reptiles has been studied by only four workers (6, 7, 9, 11). The results of Nickel's (6) investigations using alligators were published at the time this paper was in preparation and were unknown to me when this investigation was being conducted. The results of these previous investigations are not conclusive. Moreover, Schlieper (7), Wojtusiak (11), and Wagner (9) used colored papers and it is well known (10) how the differences in intensities can affect the results under such circumstances.

In the case of four species of Pacific salmon, *Oncorhynchus nerka*, *O. kisutch*, *O. keta*, *O. gorbuscha*, certain correlations between their retinal and behavioral responses have been made (1, 2, 3). It was felt that a similar investigational approach to the reptiles would be worthwhile. The purpose of this investigation was, therefore, to ascertain the retinomotor responses of the chameleon to various wave lengths and to correlate these with a behavioral response such as feeding. To accomplish this, it was first necessary to study the structure of the retina and its photomechanical responses.

Materials and Methods

Adult, unsexed, Florida chameleons (*Anolis carolinensis*) purchased from the General Biological Supply House (Turtox) were used. They show changes in coloration from bright green to dark brown. Their lengths ranged from 11 to 18 cm.

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Contribution from the Department of Zoology, McGill University, Montreal, Que., and Department of Psychology, Queen's University, Kingston, Ont. This investigation was supported by grants from the National Research Council and Queen's Committee on Research.
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The animals were kept in warm (26–32° C) and humid terraria amply supplied with vegetation. They were provided with fruit flies (*Drosophila* sp.) and in addition ate various organisms that were on the vegetation.

To investigate the rate of light adaptation 12 chameleons were kept in darkness for 17 hours preceding exposure to light. At the end of the dark period 2 specimens were collected and the remaining 10 were immediately subjected to 120 ft-c of white light. Additional dual specimens were collected at time intervals of 10, 20, 50, and 100 minutes. To investigate the rate of dark adaptation the same number of specimens were collected over the same time intervals of darkness following a 17-hour period of constant white light exposure of 120 ft-c intensity. The heads of all specimens were immediately fixed in standard Bouin's solution following the collecting intervals. The eyes were removed from the heads after 24 hours and placed in fresh solution for an additional 24-hour period. They were then imbedded in paraffin (m.p. 56° C) and sectioned at 8 μ thickness, after which they were stained in a routine manner with Harris haematoxylin and eosin.

The thicknesses of the retinal pigment layers and the cone layers were measured. Five measurements from each eye were made using a calibrated ocular micrometer. The graphs were constructed from direct measurements and from retinal thicknesses expressed as percentages.

Results

A. Thickness of the Retina

The retinae of the lizards examined during the course of this investigation showed a great deal of variation. The retinae ranged from 65 μ to 397 μ in thickness. As has been mentioned in a previous paper (1), it is not possible, unless an extensive study is undertaken, to deduce exactly how the thickness of the retina modifies the thicknesses of the various layers composing it.

B. Structure and Responses of the Retina

The retina consists of 10 layers and membranes. A prominent conus papillaris is also present (Fig. 4). There is a large fovea centralis (Fig. 3) with a high concentration of cones.

1. Epithelial pigment layer (Fig. 1). This layer is in the form of a thin strip. The pigment is distributed within the body and processes of the epithelial cells and is quite dense with the pigmented cell processes intruding between the cones. The heavily pigmented chorioid lies immediately adjacent to the pigmented epithelial layer (Fig. 2) and in some preparations it is difficult to determine the boundary between the two layers. In unstained preparations the pigment is dark brown and is not much different in color from that seen in stained preparations. This material is presumed to be melanin.

   The pigment does not undergo any movement when the dark-adapted animal is subjected to light, nor does it respond when the light-adapted animal is placed in dark (Figs. 1, 2, 7, 8).

PLATE I

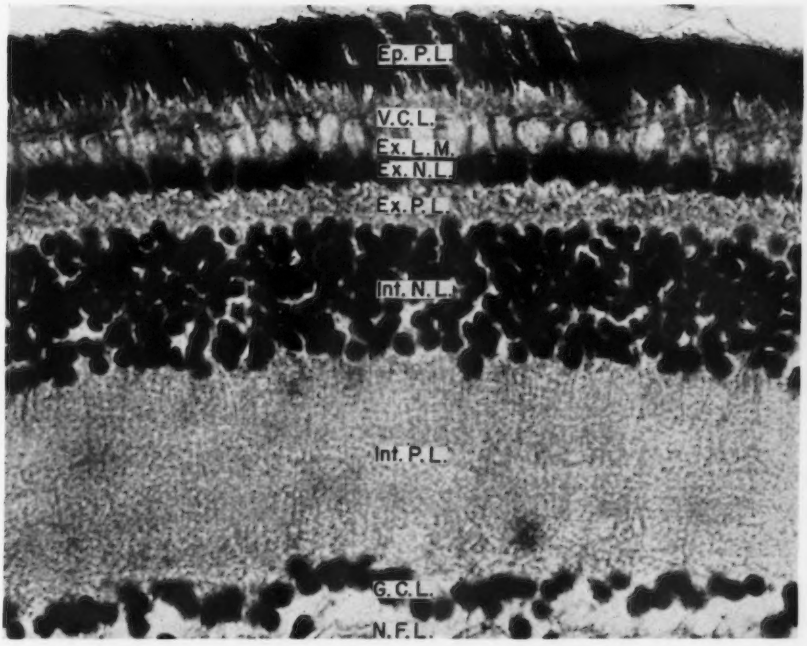


FIG. 1. Photomicrograph of a vertical section of a light-adapted retina of *Anolis carolinensis*. (×800)

Ep. P.L. Epithelial pigment layer.
V.C.C. Visual cell (cone) layer.
Ex. L.M. External limiting membrane.
Ex. P.L. External plexiform layer.
Int. N.L. Internal nuclear layer.
Int. P.L. Internal plexiform layer.
G.C.L. Ganglion cell layer.
N.F.L. Nerve fiber layer.

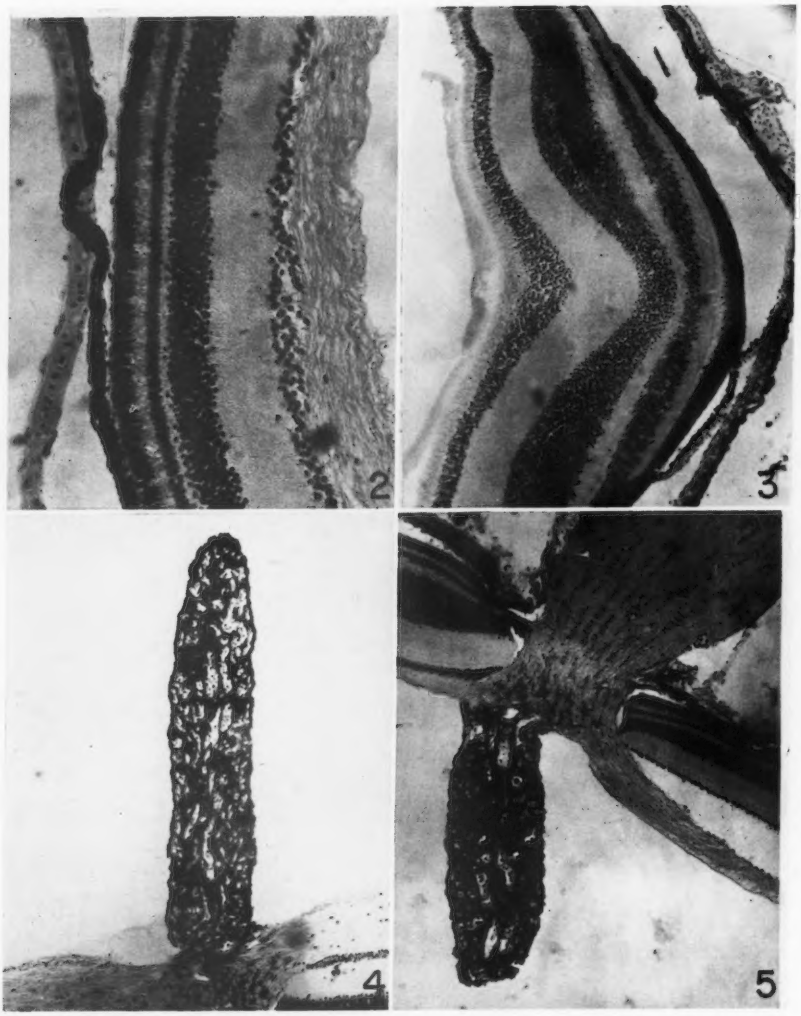


FIG. 2. Photomicrograph of a section of a dark-adapted *A. carolinensis* retina. (×170)
FIG. 3. Photomicrograph of a section showing the fovea centralis in the *A. carolinensis* eye. (×140)
FIG. 4. Photomicrograph showing the conus papillaris in the eye of *A. carolinensis*. (×120)
FIG. 5. Photomicrograph showing the region of the eye where the nerve fibers of the retina form the optic nerve. (×100)

2. Visual cell layer. The visual cell layer in *A. carolinensis* is apparently composed entirely of cones (Fig. 1) as no rods were observed. The cones may be single or double (Figs. 1, 6). No twin cones were encountered. The proportion of single cones to double cones is approximately 2:3. The notable features of the chameleon cones are: (i) the slender outer segments, (ii) fairly small, dark-staining ellipsoids, and (iii) prominent paraboloids (chromophoebic) and nuclei. The oil droplet, which is small, appears colorless and most cones were observed to possess it. Among the double cones, only the chief cones contained oil droplets, the accessory cones did not. The accessories, on the other hand, possessed large paraboloids while most of the chief cones lacked them.

   In the experiments conducted, it was observed that the cone myoids neither contracted in light nor elongated in dark (Figs. 1, 2, 7, 8). The cones of the chameleon do not appear capable of undergoing photomechanical changes.

   The cones were in rows and not arranged in any particular shaped mosaics.
3. External limiting membrane (Fig. 1). In *A. carolinensis* the retina is a thin but prominent membrane separating the cone myoids from the external nuclear layer. It is invariably very easily seen in the sections of the retina, appearing like a sieve through whose pores the cone myoids pass.
4. External nuclear layer (Fig. 1). The large and prominent nuclei of the cones which make up the external nuclear layer are dark-staining and oval to ellipsoid in shape. They lie immediately adjacent to and in close association with the external limiting membrane. No differences

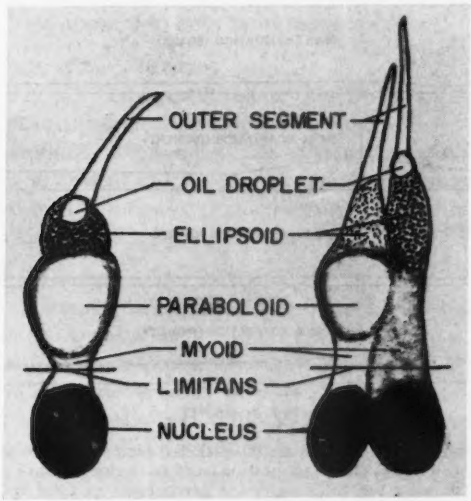
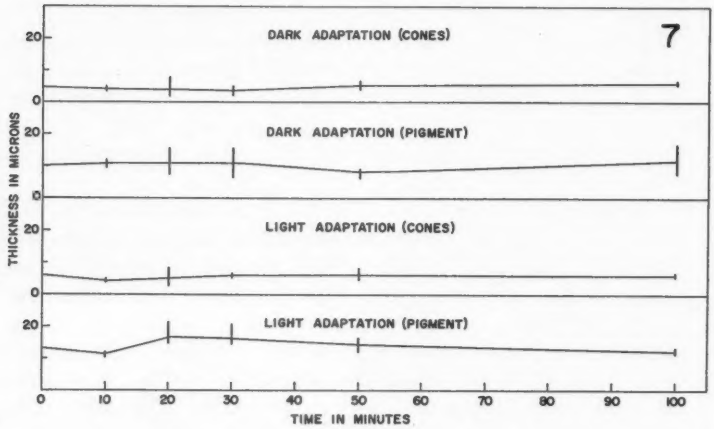


FIG. 6. Diagram of single and double cones in the retina of *A. carolinensis*. (×8000)

in staining properties were observed between nuclei of the external layers of animals exposed to light and those subjected to darkness.

The external nuclear layer of the chameleon is only one cell thick and is much thinner than the inner nuclear layer (Fig. 1).

5. External plexiform layer (Fig. 1). Some of the foot pieces of the cones are seen as darkly stained bodies in this layer. In addition, the axons and their branched ends with knobbed tips, which synapse with the foot pieces of the cones, stain well and are clearly seen. The remainder of the layer is lightly staining and transparent.



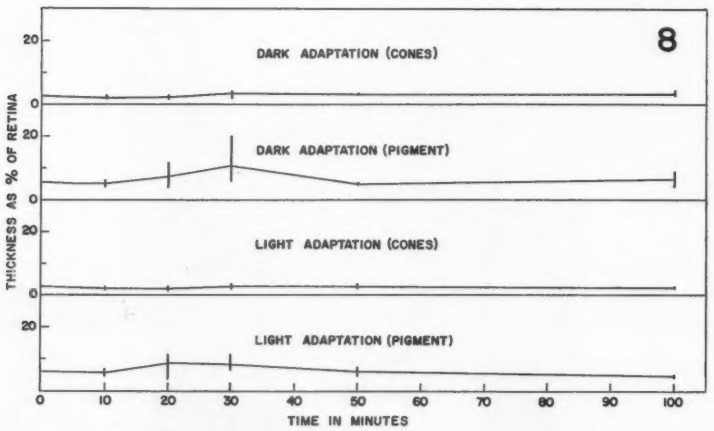


FIG. 7. Graph showing the thicknesses of epithelial pigment and cone layers at various times after exposure to light (light adaptation) and to darkness (dark adaptation).

FIG. 8. Graph showing the thicknesses (as percentages of total retinal thickness) of epithelial pigment and cone layers at various times after exposure to light (light adaptation) and to darkness (dark adaptation).

This layer is also referred to in the literature as the external molecular or reticular layer.

6. Internal nuclear layer (Fig. 1). This layer is composed of darkly staining bodies of the bipolar, amacrine, and Muellerian fiber cells.

   Compared to the external nuclear layer, the inner nuclear layer is much broader and is about 5–6 times thicker than the external nuclear layer. This layer is, however, not as dense. The internal nuclear layers of dark- and light-adapted animals do not differ in staining reactions.
7. Inner plexiform layer (Fig. 1). This is also referred to as the inner molecular or reticular layer. It is approximately four times as broad as the inner plexiform layer. The dendrites and endings of the bipolar cells, and the axons and endings of the ganglion cells synapse in this region of the retina and may be seen quite clearly. In general this is a transparent layer.
8. Ganglion cell layer (Fig. 1). This layer is composed of darkly staining large cells. It is one cell thick in most areas of the retina except in the dorsal region where it may be two and, in some cases, three cells thick. A few "parasol" ganglion cells also appear to be present in the chameleon retina. No differences between the staining properties of ganglion cells occurred between dark-adapted and light-adapted animals.
9. Nerve fiber layer (Fig. 5). The nerve fibers from the ganglion cells comprise this layer, which is thicker in the region of the fundus than in the peripheral regions. This layer is quite transparent and the individual fibers are quite clearly seen.
10. Inner limiting membrane (Figs. 2, 5). This transparent membrane, which is less prominent than the external limiting membrane, forms the innermost boundary of the retina. Unlike the external limiting membrane, this appears to be a continuous sheath.

C. Other Features of the Retina

1. Fovea (Fig. 3). Only one fovea is present in the chameleon retina and is located in the lateral part of the fundus.
2. Conus papillaris (Figs. 4, 5). The prominent, heavily pigmented conus papillaris is present in the same area of the retina where the optic nerve is formed by the union of nerve fibers from ganglion cells. The conus is highly vascularized.

D. Behavioral Responses

In general, attempts to condition the animals to display any behavioral responses upon the application of stimuli were not successful. The sluggishness of these chameleons was probably responsible for such negative response. Fruit flies were offered every day at the same time after tapping the side of the terrarium with a glass rod (vibratory stimulus). After 4 weeks of this procedure the animals still did not learn to expect food. In another experiment, a box was constructed with two chambers leading from a common space. These chambers were covered with small metal plates through which electric current could be passed. The strength and duration of the current was controlled by a

physiological electric stimulator. The purpose was to teach the animals to choose the chamber which contained a twig, or was illuminated by white light or light of a particular wave length. If the animals chose the wrong chamber they were supposed to receive an electrical shock as punishment.

It was discovered, however, that the animals choosing the wrong chamber failed to receive shocks because their feet were dry. A wet sponge was then placed in the common chamber and the animals were placed on it at the beginning of each experiment. The moisture did not, however, last long enough and, once their feet were again dry, the current failed to affect them. In addition, the animals proved to be very slow learners and tended to remain in one spot for a long time unless they were prodded. After several attempts, the experiments were discontinued due to the paucity of time. One observation of interest is that without exception, the animals that were green at the commencement of the training period turned brown upon receiving an electrical shock.

Discussion

The absence of rods, presence of a fovea, and the thick inner nuclear layer indicate that the eye of *Anolis* is undoubtedly well suited for a diurnal mode of life (10). Walls (10) has mentioned that the inner nuclear layer is much thicker in diurnal animals with cone-rich retinae than in nocturnal animals with rod-rich retinae. In the latter the external nuclear layer is thicker than the inner nuclear layer. Since no special techniques were employed it was not possible to obtain a detailed picture of the neurological arrangement within the retina. However, experience gained as a result of previous investigations (1, 3) enabled the interpretation of the retinal neurological arrangement using preparations obtained by routine methods. The inner nuclear layer being much thicker than the external nuclear layer is due to the presence of cones alone in the visual cell layer. This results in the presence of a large number of bipolar and amacrine cells which compose the inner nuclear layer.

The presence of double cones in the retina suggests it is capable of good resolving power (12). This may perhaps be due to the increase in the area covered by the cones.

The absence of retinomotor responses in the chameleon may be a result of the efficient pupillary responses that it is capable of (8). The circular pupil of this animal is capable of undergoing rapid contraction in light and dilatation in dark or dim light thus controlling effectively the amount of light entering the eye.

Some workers (4, 5) have studied the effect of light on the staining properties of nuclear and ganglion cells in the teleostean retina. The influence has been a doubtful one because Garten (5) found that in *Abramis* and *Leuciscus*, light decreased the capacity of the nuclei of the external nuclear layer to stain, but Chiarini (4) working with *Leuciscus* did not observe any differences. The results of this investigation support the latter view.

Due to the absence of retinomotor responses in *A. carolinensis* it has not been possible to correlate these responses with changes in light conditions.

The inability, so far, to obtain any behavioral responses from these animals makes it impossible to present, in a quantitative way, the effect of various light intensities and wave lengths on their vision using histophysiological and behavioral methods. It appears that the electrophysiological technique will enable one to study these aspects in detail. The absorption spectrum of the cone pigment extract (iodopsin) should also yield valuable information.

Acknowledgments

This investigation was carried out at Queen's University, Kingston, Ontario. My thanks are due to Dr. P. H. R. James of the Psychology Department for supporting it from his grants, for providing space, and for giving valuable advice. The kindness of Dr. B. N. Kropp in providing space and facilities in the Histology Department is also acknowledged. Miss Sheila L. Duff carried out the histological work and Mr. Ned Rowe took the photomicrographs. I am indebted to Mr. S. S. Peters for criticizing the manuscript.

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DEVELOPMENTAL RATES AND DIAPAUSE IN ACHETA PENNSYLVANICUS (BURMEISTER) AND ACHETA VELETIS ALEXANDER AND BIGELOW (ORTHOPTERA:GRYLLIDAE)[1]

R. S. BIGELOW[2]

Abstract

Tendencies to diapause were not observed in nymphs of *Acheta pennsylvanicus* (Burmeister), but diapause was noted in a high proportion of the nymphs of *Acheta veletis* Alexander and Bigelow. On the average, nymphal development was more rapid in *pennsylvanicus* than it was in *veletis* nymphs. Embryonic diapause always occurred in *pennsylvanicus* but never in *veletis* eggs. These differences in developmental physiology are genetically determined and the failure of the two species to produce hybrids may be due to conflicting lethal interactions of the two genotypes in hybrid embryos. Both species die out after several generations of laboratory rearing at continuous high temperatures, and the evolution of cold hardiness has apparently involved a reduction in tolerance to constant high temperatures. Reproductive isolation may have been achieved by these two species without geographical isolation. Nymphal development is more rapid in northern than in southern *veletis* populations.

Introduction

The northern spring and fall field crickets pose an interesting evolutionary problem. Sympatric over most of northeastern North America, and so similar in song and morphology that they have long been considered a single species, they are nevertheless reproductively isolated and differ distinctly in their developmental physiology. Both species survive winter conditions from Quebec westward at least to Saskatchewan, but winter survival is accomplished by a different developmental stage in each species: by the egg in *Acheta pennsylvanicus* (Burmeister), by late instar nymphs in *Acheta veletis* Alexander and Bigelow (1). This divergence in developmental physiology is not only the most striking result, but was possibly also the direct cause, of speciation in this case, as suggested by Bigelow (2) and discussed in detail by Alexander and Bigelow (1). Therefore, apart from their vital importance to the survival of insects in regions where adverse environmental conditions prevail during part of each year, developmental rhythms may be important factors in insect speciation itself.

The object of this paper is to consider the extent of developmental divergence between *pennsylvanicus* and *veletis*, the extent of such divergence between northern and southern *veletis* populations, and the bearing of such divergence on the speciation process.

[1]Manuscript received March 23, 1960.
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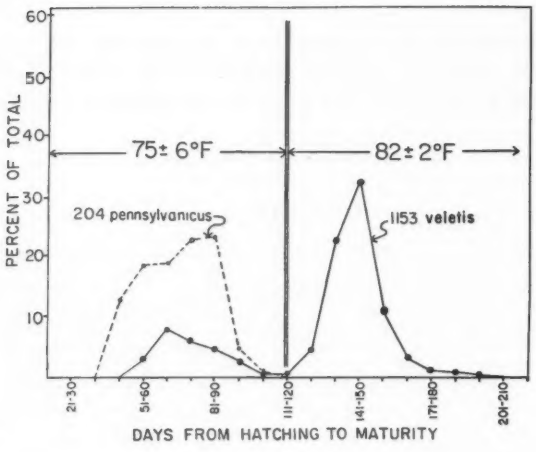

FIG. 1

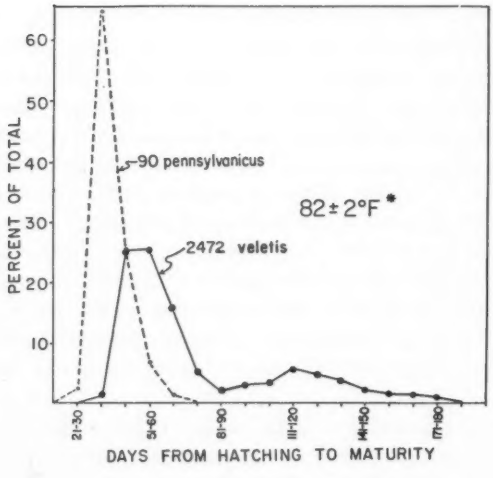

FIG. 2

NOTE: The curves of Figs. 5–9 are based on *veletis* specimens reared more or less simultaneously during the summer of 1958; those in Fig. 4 are based on specimens reared simultaneously during the winter of 1957–58. In Figs. 1 and 2 the *veletis* specimens were reared during the summer of 1958 and the *pennsylvanicus* specimens during the winter of 1957–58 at slightly lower average temperatures. In Figs. 2, 5–9 the asterisk indicates that the specimens were reared in incubators that rose above 82° F whenever the general laboratory temperature did so.

Collection of Specimens

This study is based on specimens collected from the field and subsequently reared in the laboratory. Each mention of Quebec populations refers to population samples taken originally in the field in southern Quebec within about 60 miles of Montreal. In late April, 1958, about 200 *veletis* nymphs were collected at the following localities: Danbury, North Carolina; Culpeper, Virginia; Leesburg, Virginia; Frederick, Maryland; Gettysburg, Pennsylvania. The specimens were brought to the laboratory and immature males and females of

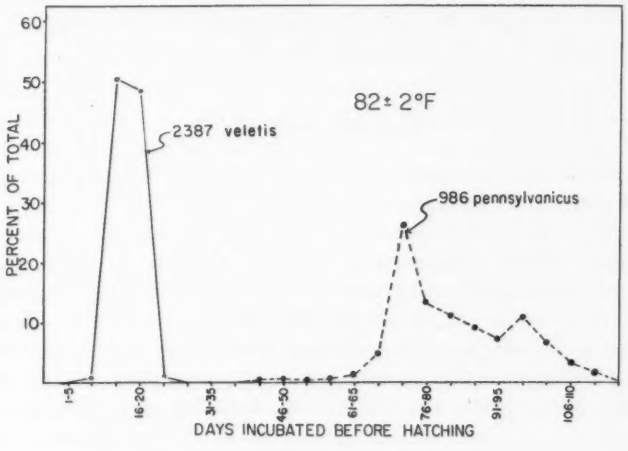

FIG. 3

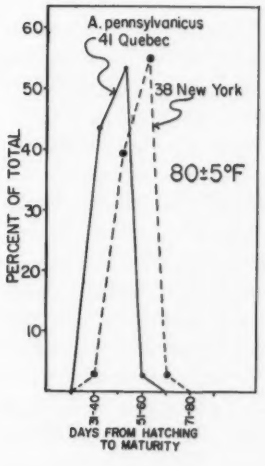

FIG. 4

all populations were segregated, and later crossed with one another and with Quebec individuals. The offspring of these crosses were reared to maturity during the summer of 1958, and the *veletis* results illustrated in Figs. 1–9 are based on these rearings.

The only *pennsylvanicus* population from outside Quebec that was involved in this study was taken from Bangall (Dutchess County), New York State, in July, 1957. The "New York" results illustrated in Fig. 4 were based on specimens hatched from eggs laid by these field-collected individuals. All *pennsylvanicus* results (Figs. 1, 2, 4) are based on first generation laboratory-reared progeny of field-collected parents; those illustrated in Figs. 1 and 2 are based on composite samples of Quebec and New York individuals.

Rearing Methods

Breeding adults were maintained either in 24×18×16 in. glass-walled cages or in 1-gal glass candy jars. Eggs were laid in moist sand, and the sand samples containing eggs were removed at frequent intervals and incubated at 82±2° F. Nymphs were reared from hatching to maturity in 1-gal glass candy jars containing strips of paper towel. All candy jars were provided continuously with glass vials containing water and plugged with cotton wool. Each glass-walled cage was provided with both sand and cotton that were kept moist through a wick of cotton wool that led upward from a water reservoir. An excess of dry baby rabbit pellets was continually available as a food supply to all specimens.

Temperatures at various locations within the laboratory were recorded from maximum and minimum thermometers and continuous temperature records were made with recording thermometers. Nymphs were reared both at laboratory temperatures and in incubators maintained at 82° F and above. These incubators were not equipped with refrigerating units and therefore temperatures within them rose with the general temperature of the laboratory whenever this exceeded 82° F. Eggs were incubated in B.O.D. incubators, equipped with both heating and refrigerating units, which remained at 82±2° F at all laboratory temperatures. All the results illustrated in Figs. 5–9 were based on specimens reared more or less simultaneously during the summer of 1958.

The number of nymphs per jar varied from about 25 to slightly over 100. The more crowded jars were provided with a greater area of paper towel and the proportion of crowded and less crowded jars was approximately the same for all strains. All jars were checked daily, or every second or third day, and adults were removed as they appeared. Detailed maturation records were kept for each jar until all living specimens had matured. In no case was a partial record, involving only a portion of the nymphs originally placed in a jar, used in the compilation of the results compared below; in every instance the full range of individual variation was taken into account.

Effect of Crowding on Rate of Development

During the summer of 1959 the following experiment was carried out to determine whether or not rate of development was seriously affected by the number of specimens per jar. All nymphs used in this experiment hatched on July 23, 1959. Two strains were used: a *veletis* strain descended from specimens collected at Frederick, Maryland, in April, 1958, and an *assimilis* strain descended from specimens collected in Jamaica in April, 1959.[3]

One-gallon glass candy jars were provided with equal areas of paper towel, a constant water supply, and an excess of dry baby rabbit pellets. Specimens of each strain were placed in these jars as indicated in Table I.

Table I shows clearly that mortality was higher in the more crowded cultures, and suggests that crowding tends to retard development (at least in *Acheta assimilis*). There was, however, no striking retardation of development at higher densities and in the case of *veletis* (the only species of the two to be considered further here) the maturation peak occurred during the same 10-day period at all densities. If all northern specimens in the 1958 experiments, for example, had been reared at low densities and all the southern specimens at high densities it is possible that the less extreme differences in time of occurrence of maturation peaks may have been due to crowding. However, both the northern and the southern strains were reared at both high and low densities in the 1958 experiments. The high density cultures referred to in Table I contained no more paper towel than the low density cultures, but in the 1958 rearings the more crowded jars were provided with additional space (paper towel). It is therefore very unlikely that the differences in rate of development to be discussed below were due to crowding.

TABLE I

Results of crowding experiment. The figure opposite each period of nymphal development refers to the number of specimens (not to the percentage of the total number of specimens) which matured during that period

	Acheta veletis per jar					*Acheta assimilis* per jar				
	1	2	10	25	100	1	2	10	25	100
Days from hatching to maturity										
31– 40									1	
41– 50						9	7	10	17	15
51– 60			1	1	9	1				32
61– 70	6	7	5	9	32		1			11
71– 80		3	1	5	5					1
81– 90				2	6					
91–100	1				3					
Over 100	2		1	2	5					1
Percentage mortality	10	0	20	24	40	0	20	0	28	40

[3]This species (*Acheta assimilis* F.) is not the species discussed in a previous paper (Bigelow (2)), which dealt with *pennsylvanicus*, *veletis*, and *rubens* only.

Acheta pennsylvanicus and *A. veletis*

Since the summer of 1956 thousands of *veletis* and *pennsylvanicus* nymphs have been reared in the laboratory, at various temperatures and during all seasons. During the later instars most *veletis* nymphs enter a state of retarded development that has not been observed in *pennsylvanicus* nymphs. Even at temperatures constantly above 80° F a significant proportion of *veletis* nymphs enter this state, as shown in Fig. 2, when about 30% required more than 90 days from hatching to maturity, and a few required a full 6 months; all *pennsylvanicus* nymphs matured in less than 70 days. Over 60% of the *pennsylvanicus* nymphs reared at this temperature matured in 31 to 40 days;

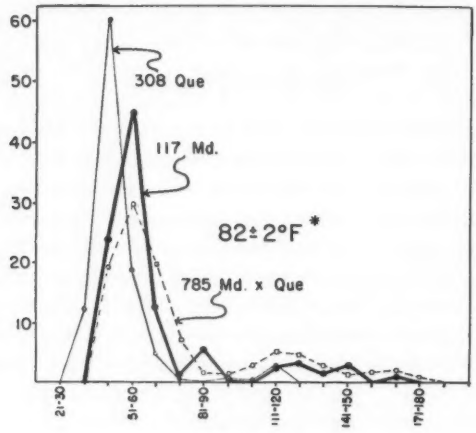

FIG. 5

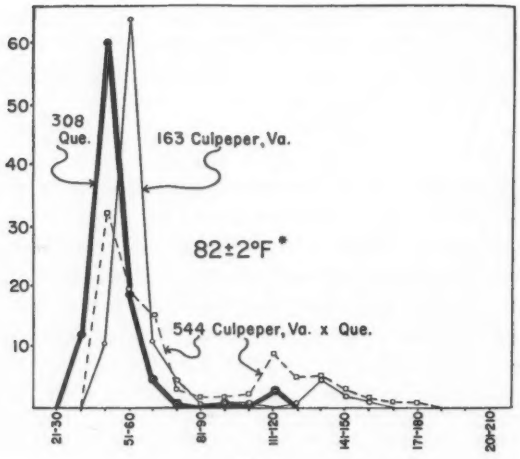

FIG. 6

only 1.6% of the *veletis* nymphs matured in less than 40 days. Actually, the *veletis* nymphs of Fig. 2 experienced higher temperatures than did the *pennsylvanicus* nymphs. The *veletis* specimens were reared during the summer of 1958 when the temperature of the laboratory was above 82° F for about 384 hours between May 12 and August 31; the *pennsylvanicus* specimens were reared in the winter when the laboratory temperature never exceeded 82° F. Had the two species been reared simultaneously in the same incubators the difference between their developmental rates would have been even greater than that apparent in Fig. 2. When reared at mean daily temperatures above 80° F, most (80–90%) *pennsylvanicus* nymphs mature within a 2-week period, and

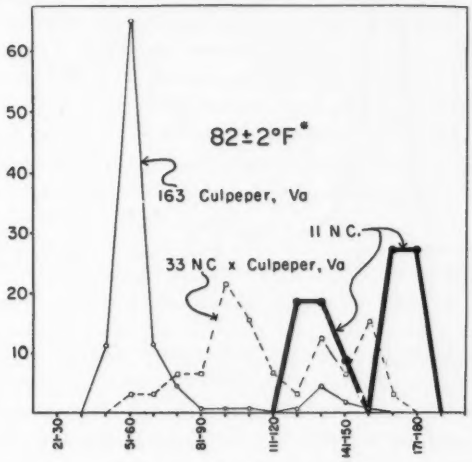

FIG. 7

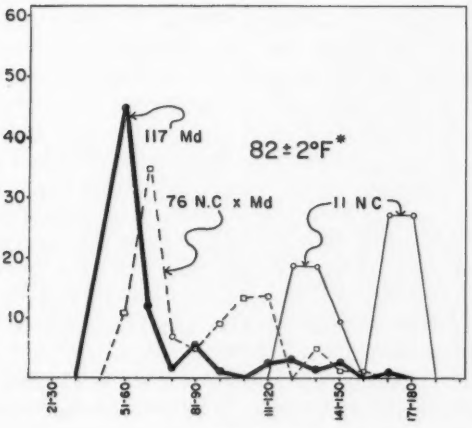

FIG. 8

the entire range of individual variation rarely exceeds 30 days. This is apparent in Fig. 4 as well as in Fig. 2. At comparable (or even higher) temperatures, *veletis* nymphs often differ as much as 4 months in the times required from hatching to maturity, and this extreme variability appears to be a characteristic of the species as a whole, as shown in Figs. 5–9.

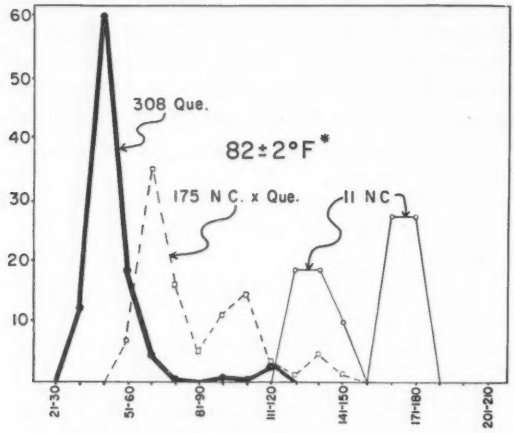

FIG. 9

At lower temperatures most *veletis* specimens require more than 4 months in the nymphal stage. At mean daily temperatures of about 75±6° F less than 26% of 1153 *veletis* specimens matured in less than 4 months. All of 204 *pennsylvanicus* specimens matured within 4 months and over 90% matured in less than 3 months at comparable temperatures, as shown in Fig. 1. Again, the *veletis* specimens were reared during the summer of 1958 while the *pennsylvanicus* were winter-reared in the laboratory. Judging from the rate of development in stock *veletis* cultures, most of the *veletis* specimens of Fig. 1 would have remained immature for over 10 months had they not been transferred to incubators maintained at 82° F. At lower temperatures increasing proportions of *veletis* nymphs fail to mature during a period in which all *pennsylvanicus* nymphs mature, and the difference in developmental rates tends to approach, or even to exceed, the point where the curves for the two species no longer overlap. Clearly, nymphal development is less rapid and nymphal diapause is more prevalent in *veletis* than in *pennsylvanicus*.

The rate of development during the egg stage of the two species is strikingly different, even at constant high temperatures. At 82° F about 98% of *veletis* eggs hatch within a 7-day period, after incubating for about 2 weeks. At the same temperature *pennsylvanicus* eggs begin to hatch only after a full month of incubation, and most require from $2\frac{1}{2}$ to 4 months.

In each species individual variation is marked in the overwintering stage, slight in the non-overwintering stage. At 82° F individual *veletis* nymphs differ by more than 4 months in the times required from hatching to maturity;

individual *pennsylvanicus* eggs differ more than 2 months in the times required from laying to hatching. At the same temperature the form of the curve for *pennsylvanicus* nymphs is not unlike that for *veletis* eggs. It is significant that development is retarded in the overwintering stage of each species even at unnaturally high laboratory temperatures, and at all seasons. These developmental rhythms are clearly inherent, genetically determined, and obligate in each species. Genetical divergence between the two species appears to be approaching an extreme. All *pennsylvanicus* individuals possess genes that produce diapause in the egg stage, but no *veletis* individuals possess such genes; genes that produce nymphal diapause are present in at least most *veletis* individuals, but appear to be absent in all *pennsylvanicus* individuals. The survival of either species in northern regions clearly requires the maintenance of a set of genes that differs from the comparable set in the other species, and the contamination of either set with genes from the other species would almost certainly produce disadvantageous results. An efficient mechanism for the prevention of gene exchange is therefore essential, and the maintenance by each species of its own distinctive diapause characteristics despite sympatry over vast areas of northern and eastern North America testifies that such a mechanism does, in fact, exist.

The most obvious factor preventing an interchange of genes is the seasonal difference in the breeding seasons of the two species, but although this difference is striking, it does not completely isolate breeding adults at all times (see Alexander and Bigelow (1)). During late July and (or) early August mature adults of both species are in contact throughout most of northeastern North America. If genes are exchanged during this period, then it is reasonable to expect a tendency toward diapause in a certain proportion of the eggs laid by *veletis* females and a tendency toward absence of diapause in certain *pennsylvanicus* eggs. Indirectly, the extent of overlapping in the incubation periods of eggs laid by the two species might be taken as a measure of the extent of gene exchange between them.

Since 1956 at least 100,000 eggs of each species have been incubated in this laboratory. During the summer of 1958 alone 20,155 *veletis* eggs hatched at 82° F, not one of which required more than 30 days of incubation. However rapidly or slowly they developed from hatching to maturity in the laboratory, whatever the conditions of temperature, crowding, or light: dark ratio at which they were reared, and whether they were derived from North Carolina, Virginia, Maryland, Pennsylvania, or Quebec, *veletis* females always laid nondiapause eggs. After hatching had apparently ceased, examination of *veletis* egg samples revealed only empty shells and dead eggs, and egg samples incubated for months beyond the normal *veletis* incubation period produced no further nymphs. Similar numbers of *pennsylvanicus* eggs, laid at all seasons and under a similar variety of conditions, were incubated at various temperatures and not one *pennsylvanicus* egg hatched in less than 30 days, even at constant temperatures as high as 82° F. At this temperature, most required over 70 days of incubation (five times the normal *veletis* incubation period at

the same temperature). Even after months at low temperatures, *pennsylvanicus* eggs still required approximately 2 weeks at 82° F. The incubation periods of eggs of these two species do not overlap at all, and show no indication of gene interchange; the genes that determine the rate of embryonic development apparently differ distinctly.

Repeated attempts to obtain *veletis* × *pennsylvanicus* hybrids in the laboratory have failed (see Alexander and Bigelow (1)). Other species, differing in both song and morphology, have produced interspecific hybrids in large numbers (see Bigelow (3)), but despite their apparent identity in song and morphology, and despite interspecific copulation, these two species have failed to produce a single hybrid offspring. In at least one instance *pennsylvanicus* sperms reached the spermatheca of a *veletis* female (Bigelow (2)), and it is therefore possible that interspecific fertilization occurs, but fails to produce viable embryos. If so, an interaction between *pennsylvanicus* genes tending to inhibit and *veletis* genes tending to accelerate embryonic development may result in the death of the hybrid embryo. Divergence in developmental physiology may have thus produced a most effective form of reproductive isolation, and such divergence might therefore be an important step in the speciation process in certain cases.

The time of appearance of *veletis* adults in the field varies with the season in Quebec (June 10 in 1956, mid-May in 1957, 1958, 1959), but in normal years oviposition will not occur before late May or early June when the mean temperature of the soil is probably not above 70° F. At such temperatures *veletis* eggs require about a month of incubation, as shown in Table II, and therefore *veletis* nymphs probably do not appear in the field before late June or early July.

TABLE II

Incubation periods of *Acheta veletis* eggs at various temperatures

Temperature in °F	Days of incubation before hatching	
	Range	Mean
Daily mean 68	28–47	35
" " 73	18–35	20
" " 75	16–20	18
Constant 73±2	17–34	20
" 75±2	12–24	17
" 82±2	9–30	14
" 91±2	9–16	11

Probably only a small fraction of *veletis* nymphs mature before winter begins, for at mean daily temperatures of 75° F less than 5% mature within 60 days (i.e. before September in the field). Any that mature in the fall are probably winter-killed, for collecting in very early spring has so far revealed many late instar nymphs, but no living *veletis* adults (and no singing males have been heard) anywhere from Quebec to North Carolina. Any eggs laid in the fall by

veletis individuals, and any nymphs that might hatch from such eggs, are probably also winter-killed, for both eggs and early instar nymphs of this species are unable to survive temperatures just above freezing for more than a week in the laboratory. During July and August *veletis* nymphs have ample opportunity to reach the cold-resistant later instars, and the inherent diapause tendencies coupled with cool September temperatures (in Quebec) probably prevent the majority from overpassing this winter-resistant stage.

In *pennsylvanicus*, adults appear in the field rather suddenly in late July and early August. Eggs are laid during August and September, and probably only a minute fraction (if any) hatch before the onset of winter. Since the incubation period of this species is well over a month at 82° F, even eggs laid in early August will not hatch before September and very few such eggs would hatch before October. Any *pennsylvanicus* nymphs that hatch in the fall are probably winter-killed. Embryos that have passed beyond the diapause stage are probably also winter-killed since after long periods at low temperatures *pennsylvanicus* eggs uniformly require 2 weeks above 75° F before incubation is complete. A small proportion require more, but none hatch in less than 2 weeks, which suggests that all embryos beyond the diapause stage at the onset of low temperatures are killed by these temperatures, and that the diapause stage itself occurs early in embryonic development. Diapause is apparently determined by genes in the embryo rather than by cytoplasmic or yolk constituents provided by the mother, for *pennsylvanicus* × *assimilis* hybrid embryos developed without diapause even in eggs laid by a *pennsylvanicus* female (Bigelow (3)).

Quebec populations of either *pennsylvanicus* or *veletis* are difficult to maintain in the laboratory at constant high temperatures (over 75° F) for more than three or four generations. Fecundity and vigor appear to decrease in successive generations until the third or fourth laboratory-reared generation usually dies out altogether.

Casual observations suggest that low temperatures during the diapause stage of either species tend to increase the fecundity of the resulting adults, and populations of either species from regions south of Quebec can be maintained for longer periods at constant high temperatures than can Quebec populations. A *pennsylvanicus* strain from Dutchess County, New York State, has been reared in this laboratory since July, 1957 (2½ years) and although their fecundity has decreased they are still maintaining themselves. The same is true of *veletis* populations from Maryland, Virginia, and North Carolina. One *veletis* strain, collected in Virginia in March, 1957, has survived for 3 years in the laboratory.

These differences in high temperature tolerance between northern and southern populations of both species suggest that low temperature requirements may be the major factor involved in limiting the southern distribution of the two species. Neither occurs south of a line corresponding roughly with the southern border of North Carolina, and the evolution of cold hardiness in both species has apparently involved a sacrifice of the capacity to tolerate constant high temperatures (i.e. to exist in regions of very mild winters).

Conversely, field cricket species that do not require periods at low temperatures and are thus able to exist where winters are very mild, are not able to survive where winters are severe. The only *Acheta* species that survive in the field north of a line corresponding roughly with the southern boundary of Pennsylvania are *pennsylvanicus* and *veletis*. It appears, then, that no genotype has yet evolved in the genus *Acheta* which provides high temperature tolerance and cold hardiness simultaneously in a single gene pool, or species.

Northern and Southern Populations

Where the function of winter survival is confined to a single life history stage, as it is in both *veletis* and *pennsylvanicus*, it is obvious that development during the summer must proceed at a rate that will produce the winter-resistant stage in sufficient numbers at the proper time. If development is either too slow or too rapid the resistant stage will not be reached, or it will be overpassed, when winter begins and the resulting non-resistant individuals will be winter-killed. Rigorous selection, therefore, will eliminate individuals whose inherent rates of development do not correspond with the seasonal rhythms of the regions in which they occur. Where summers are short and winters long, individuals that develop too slowly during the summer will be eliminated during the winter and rapid developmental rates will be favored. Where summers are long, such rapidly developing individuals will overpass the cold resistant stage to perish during the winter, and slower developmental rates will be favored. If this line of reasoning is correct, rate of development should be more rapid in northern than in southern populations.

The developmental rates of *pennsylvanicus* nymphs from Quebec were compared with those of a population from Dutchess County, New York State, and the results are illustrated in Fig. 4. The curves in Fig. 4 are practically identical in shape but the New York specimens required, on the average, 10 days longer than did the Quebec individuals. The New York population was taken from a region about 300 miles south of Quebec where the growing season is slightly but distinctly longer. The number of specimens involved in this experiment is not large, but the apparent difference is probably real. Individual variation in rate of nymphal development is far less in *pennsylvanicus* than it is in *veletis* and smaller samples are required for accurate representation. Both the Quebec and the New York strains were the progeny of field-collected parents and both were reared together at the same time and under the same conditions.

Due to the extreme individual variation in all *veletis* populations large samples are required in order to represent both the rate of development and the proportion of individuals that enter diapause. At least 50, and preferably over 100, specimens of this species should be reared in order that the true distribution of variation in developmental periods can be estimated accurately.

As shown in Figs. 5 and 6 the maturation peak for Quebec specimens occurred 10 days earlier than the corresponding peaks for the Maryland and Culpeper, Virginia specimens. Unfortunately, only 11 specimens of the southernmost

(North Carolina) population were reared to maturity at 82° F in the summer of 1958. All 11 of these specimens spent over 4 months in the nymphal stage, or 2 months longer than did the majority of the Quebec, Maryland, and Culpeper individuals. Although this small sample fails to represent the true developmental characteristics of the North Carolina population as a whole, it probably reflects a real and marked difference between the rates of development of northern and southern populations. This possibility becomes more likely when the developmental rates of hybrids between the North Carolina and the Quebec, Maryland, and Virginia populations are considered. In each case, "half-North Carolina" hybrids developed much more slowly than did the pure northern parental strains, and a total of 284 of these hybrids were involved.

A total of 67 pure North Carolina nymphs were reared from hatching to maturity at 82° F and above during the summer of 1959; 12% of these specimens matured after 51–60 days of nymphal development, 19% after 61–70 days, 25% after 71–80 days, 12% after 81–90 days, and 32% required over 250 days. These results cannot be compared with those obtained in 1958 because the specimens used were descended from laboratory-reared parents and because laboratory temperatures were above 82° F for 527 hours during July of 1959 but only for 190 hours during July of 1958. It is worth noting, however, that even at higher 1959 temperatures the maturation peak of the "non-diapause" individuals did not occur until after 71–80 days, and the extreme bimodality shown by these North Carolina individuals is certainly interesting. Although 68% of these specimens matured in less than 3 months, 38% required more than 250 days. The retarded group remained immature for more than 5 months after the last specimen of the "non-diapause" group had matured. The retarded individuals hatched at the same time and from the same egg samples as the unretarded individuals; they experienced the same temperatures in the same incubator and even in the same jars. The difference between the retarded and unretarded groups is clearly genetically based. All the curves of Figs. 5–9 show a distinct bimodality, but none show such an extreme difference as this between retarded and unretarded individuals. Further study is required before this phenomenon can be clearly understood, but it appears that the southernmost *veletis* populations are not only slower to develop on the average but also contain a high percentage of individuals in which development is more spectacularly retarded than it is in northern individuals.

Discussion

Acheta pennsylvanicus and A. veletis

The difference in developmental physiology between these two species is most striking. The capacity to overwinter has been concentrated in a different developmental stage in each species, and any gene exchange at the present time would probably be detrimental to both species. Reproductive isolation is apparently complete, and yet the two species are extremely similar in song and morphology, and are sympatric over most of northeastern North America.

Their similarity and sympatry, and the fact that the only striking difference between them involves overwintering mechanisms which tend to seasonally isolate breeding adults, suggests that speciation may have been achieved without the aid of geographical isolation, as discussed by Alexander and Bigelow (1).

The major difficulty in any theory of sympatric speciation involves an explanation of the way in which genetic divergence can be initiated and increased despite a continuous exchange of genes. Such an exchange of genes will take place between individuals of any single species unless breeding individuals are unable to meet one another in the field. Any flow of genes between two populations will tend to break down genetic divergence between them, and to prevent this divergence from reaching the crucial point at which hybrid breakdown will occur. The most obvious factor that will prevent gene exchange between intraspecific populations is spatial isolation. Gene exchange between populations on different islands, for example, or on different continents, is often so slight that genetic divergence can proceed unhindered by contamination through an influx of "foreign" genes. If spatial isolation is maintained for a sufficiently long time, or if divergence is sufficiently rapid, the genetic divergence between the two populations may reach the point where hybrid sterility or inviability will prevent a free exchange of genes even in the absence of spatial isolation. At this point speciation will have been completed.

Spatial isolation, however, is not the only factor that can prevent contact between breeding individuals. Isolation in time can be equally effective, provided the breeding adults of one population are all dead before those of the other population are mature. Temporal isolation, furthermore, can occur rather suddenly if two developmental stages, widely separated in the life cycle of a single species, are more resistant to adverse seasonal conditions than are the intermediate stages of the same species. A gradual increase in the severity of winter will eliminate increasing proportions of the non-resistant intermediate stages to the point where only eggs, for example, and late instar nymphs are alive in the spring. If all the overwintered nymphs mature, mate, and die before the overwintered eggs produce breeding adults, no exchange of genes whatsoever can occur between the two populations. Individuals of both populations may live under the same stones, and share the same blades of grass as food, yet they will be prevented from interbreeding as effectively as if they were on different continents. However free the exchange of genes may have been during the gradual increase in winter severity, all gene exchange will cease at this time. The same result might be achieved through a gradual northward migration as readily as through a gradual increase in winter severity.

Although temporal isolation may appear rather suddenly in such cases, its appearance could also be gradual. Gene exchange will not be detrimental while both overwintering stages are able to survive winter conditions. When gene exchange begins to reduce the cold resistance of either overwintering

stage, or to produce hybrids with developmental rates that fail to produce the overwintering stage at the proper time, selection will act against "interpopulation" matings. Individuals that "outcross" will leave fewer progeny. Detrimental effects of gene exchange will be eliminated annually by winter-kill and the genetic "purity" of the two kinds of survivors will tend to be greater with each successive spring, until intrinsic isolation is achieved.

If cold resistance was very slight in all the intermediate stages of the original parent species, practically complete temporal isolation may appear very suddenly, before winter conditions become severe enough to eliminate either cold-resistant stage. Once gene exchange is prevented through temporal isolation, the cold resistance of the overwintering stage of each of the two populations can be increased by selection without inhibition due to an influx of genes from the other population. Divergence will then be free to proceed rather rapidly to the point where hybrid embryos, for example, are inviable.

The bulk of the available evidence favors allochronic speciation, along lines generally similar to those discussed above in the case of *pennsylvanicus* and *veletis*, and the same general process may have been the major factor in the formation of many other insect species, as proposed by Alexander and Bigelow (1).

Northern and Southern veletis Populations

Developmental rates are more rapid in northern than in southern *veletis* populations. In the north, *veletis* nymphs develop rapidly and reach the diapause stage before winter begins. In the south, *veletis* nymphs develop more slowly and do not overpass the diapause stage before winter begins. These developmental differences are genetically determined, and therefore involve the maintenance of different gene combinations. Genes that produce rapid development in Quebec populations will gradually lose their selective advantage as they are transported southward in slow, "bucket-brigade" fashion, until they become detrimental in North Carolina populations. Similarly, North Carolina genes will tend to lose their selective advantage as they are transported northward. Gene exchange between these two *veletis* populations is probably inhibited by selection as well as by distance.

In all the *veletis* populations studied the distribution of the duration of nymphal development is distinctly bimodal (or perhaps trimodal in certain hybrid strains). This suggests, although it does not, of course, prove, that a single pair or series of alleles at a particular locus trigger the diapause condition. Some of these alleles seem to initiate diapause even at temperatures above 80° F, while others appear to be ineffective at such temperatures. In the North Carolina strain a high proportion of individuals seem to carry an allele that inhibits nymphal development for very long periods despite high temperatures.

In all *veletis* populations it is also clear that the duration of nymphal development approaches a normal distribution in all "non-diapause" individuals. This suggests that the rate of development is itself determined by a large

number of factors (including genes), and that intermediate developmental rates in hybrid strains are due to the interaction of different groups of these developmental-rate genes.

Variability in the rate of development is probably required as a safeguard against annual variations in summer temperatures and the time of appearance of winter conditions.

Conclusions

Nymphal development is more rapid in *Acheta pennsylvanicus* than in *A. veletis*. Nymphal diapause does not occur in *pennsylvanicus* but does occur in most, if not in all, *veletis* individuals at mean temperatures below 75° F. Tendencies to diapause are absent from all *veletis* eggs but present in all *pennsylvanicus* eggs. These differences are genetically determined and gene exchange between the two species would probably produce detrimental effects if it occurred. Hybrid embryos may be inviable as a result of the interaction of opposing sets of genes from the two parent species. Reproductive isolation may have been produced by allochronic rather than by allopatric speciation. Rate of nymphal development is more rapid in northern than in southern *veletis* populations.

Acknowledgments

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POLYCHAETOUS ANNELIDS FROM THE SHALLOW WATERS AROUND BARBADOS AND OTHER ISLANDS OF THE WEST INDIES, WITH NOTES ON LARVAL FORMS[1]

JOAN RATTENBURY MARSDEN

Abstract

Thirty-four species of polychaetous annelids, belonging to 16 families, are reported. Most of them come from the West Indian Island of Barbados but some were collected also, or only, in Jamaica. All are coastal, shallow water forms. Observations on the life history and in particular on larval forms are included when pertinent. Zoogeographical implications are considered briefly.

Introduction

Most of the polychaetes reported here were collected in Jamaica during the summers of 1953 and 1954 and in Barbados during the summers of 1955–57. The Jamaica collection is fairly large but the bulk of it remains in the Science Museum at the Institute of Jamaica and is not immediately available for study. The Barbados specimens are the result of casual collecting done incidental to other projects in progress at the time and undoubtedly represent only a small fraction of the total polychaete population in this area. In spite of the fragmentary nature of these studies it seems wise to report them at this time together with observations on the life history and habits of some of the animals concerned since, with the establishment of biological stations in both Barbados and Jamaica, marine biological research has started and will continue on these islands and references for the identity and habits of the local fauna are few and inadequate.

The shallow waters around the island of Barbados provide a series of habitats which are either intertidal or variations on the coral reef and associated sand bottom. The intertidal shoreline offers a variety of conditions ranging from sand through gravel, stones, and boulders to cliffs and platforms of rock. The reefs vary in size, in proportion of dead to living coral, and decidedly in the dominant forms of associated plant and animal life. That other distinctly different tropical marine habitat, the mangrove swamp, although abundantly present on Jamaica and many other West Indian Islands, is absent from Barbados.

The marine polychaetes reported here fall into four categories. The first and largest of these is the group of typically tropical species, often circumtropical in distribution, which have either been described from the West Indies before or, although previously unknown in this area, are definitely to be expected. The second category includes those cosmopolitan species not restricted to warm waters. The third is a category of unexpected forms, species previously known as having a restricted range outside the Caribbean. In this report there are several Pacific species which fall into this group,

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Contribution from the Department of Zoology, McGill University, Montreal, Que.

such as *Eunice tridentata*, *Pectinaria chilensis*, and *Phragmatopoma californica*. Fourthly and finally there are a number of rare forms which are curiosities wherever they are found. This group includes the genera *Dispio*, *Magelona*, and *Ancistrosyllis*.

This collection of adult polychaetes was made during the course of a systematic study of the plankton netted off the west coast of Barbados. A number of polychaete larvae were found in these plankton collections and attempts were made to rear them to older and more easily recognized stages. Any information on larvae of forms belonging to the families discussed here is added to the text in connection with the family concerned.

Representatives of the following 16 families are included in this account: Polynoidae, Amphinomidae, Phyllodocidae, Pilargiidae, Syllidae, Nereidae, Eunicidae, Arabellidae, Spionidae, Chaetopteridae, Magelonidae, Pectinariidae, Sabellariidae, Terebellidae, Sabellidae, and Serpulidae. Thirty-one species are reported as well as three species of uncertain identification.

Taxonomic Account

Family POLYNOIDAE

HALOSYDNA LEUCOHYBA Schmarda, 1861

Halosydna leucohyba Webster, 1884, 309–310, Pl. 7, Figs. 16–18, Pl. 8, Figs. 19–20 (50); Rioja, 1946, 193 (40); Hartman, 1951, 18 (26)

Six specimens were collected at Speightstown, Barbados, from debris in cavities in old coral in about 8 ft of water.

This species is well known from Bermuda and the West Indies.

Family AMPHINOMIDAE

EURYTHOE COMPLANATA (Pallas), 1766

Aphrodita complanata Pallas, 1766, 109–112, Pl. 8, Figs. 19–26 (38)
Eurythoe complanata Monro, 1933, 245 (32); Hartman, 1940, 202–203, Pl. 31, Figs. 1–4 (22); Hartman, 1951, 25, Pl. 4, Fig. 2 (26)

This species was found at Sandacres, Hastings, and River Bay in Barbados and at Don Christopher's Cove, Quaco Point, Portland Point, and Innes Bay in Jamaica. Most specimens were taken from under small stones in shallow water on gravel or sand. It seems to be most abundant just below mean low tide level.

Eurythoe complanata has been found to be sexually mature in June and July. The ova appear white when viewed singly, slightly pinkish when seen in a group. Mature individuals have spawned in the laboratory and artificially fertilized groups of eggs have been reared for as long as 19 days. The germinal vesicle breaks down at fertilization and cleavage is complete. The trochophore is umbrella-shaped (Fig. 1) with an elongate posttrochal region. Larvae maintained longer than 14 days tended to reduce the size of the pretrochal hemisphere, to sink to the bottom, and to begin to crawl. None of the crawling forms survived more than 1 or 2 days and normal metamorphosis was not seen in the laboratory.

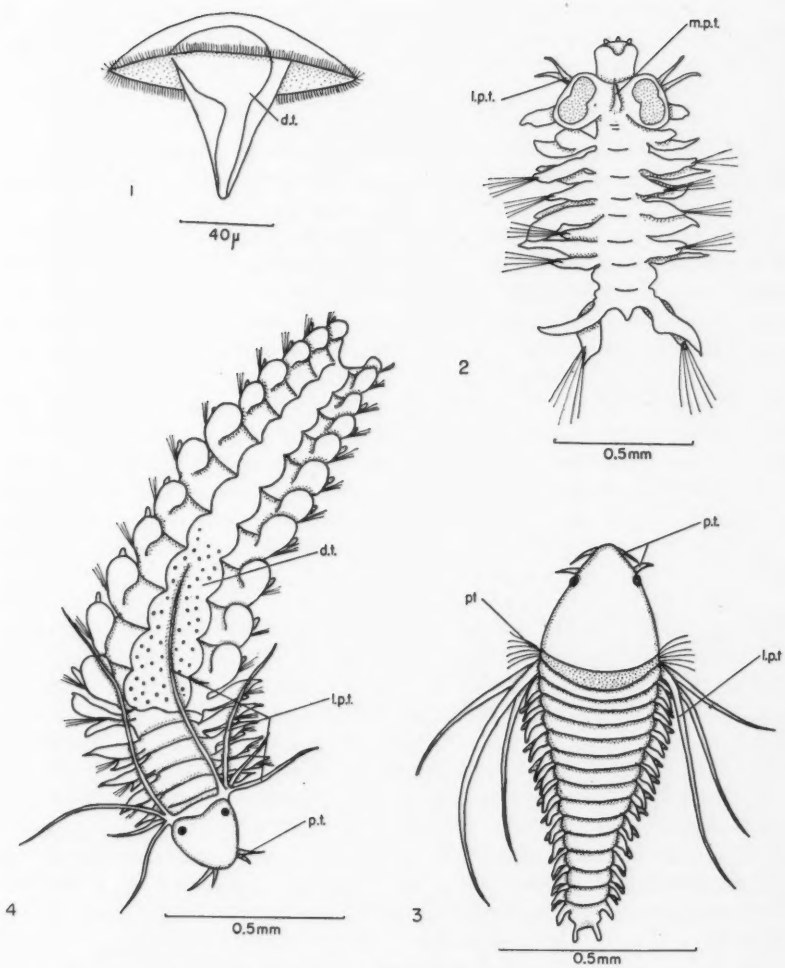


FIG. 1. *Eurythoe complanata*. Trochophore larva, 10 days old.
FIG. 2. Phyllodocid larva from the plankton, first type.
FIG. 3. Phyllodocid larva from the plankton, second type. A young posttrochophore.
FIG. 4. Phyllodocid larva, second type. An older form with 17 setigers.

ABBREVIATIONS: d.t. = digestive tract, l.p.t. = lateral prostomial tentacles, m.p.t. = median prostomial tentacles, pt = prototroch, p.t. = prostomial tentacle, pe.t. = peristomial tentacle.

This species is always a bright orange-pink color with red branchiae. It is well known from both sides of tropical America, in the eastern part of the Gulf of Mexico and in the Caribbean Sea. It is found on the Pacific coast as far north as southern California.

HERMODICE CARUNCULATA (Pallas), 1766

Aphrodita carunculata Pallas, 1766, 102–106, Pl. 8, Figs. 12–13 (38)
Hermodice carunculata Mullin, 1923, 44–45, Pl. 5, Figs. 2–3 (34); Hartman, 1951, 22–25, Pl. 5, Fig. 1 (26)

This is a common and abundant species and has been collected in Barbados at Needham Point, Carlyle Bay, Pelican Island, Bathsheba, Sandacres, River Bay, Hastings, Conset Bay, Six Men's Bay, and Paynes Bay. In Jamaica the same species has been found at Ocho Rios, Port Antonio, Drunkenman's Cay, Innes Bay, Montego Bay, Port Royal, and Morant Point. It has also been taken at Arnos Vale, Tobago, and Cato Bay, Grenada.

In *H. carunculata* the color of the dorsal surface varies from brown through tan to pink or green. The branchiae are a bright red, the ventral surface is usually a pale tan. Dorsally, individual segments are separated from one another by narrow, dark stripes. Both the branchiae and the caruncle may be striped with white. The largest specimen taken was about 35 cm long and another, somewhat larger, was seen but not taken. Most specimens, however, are much smaller, usually ranging between 8 and 15 cm.

This species was found in large numbers both on the living reef and under stones in shallow water inshore of reefs. In the latter case the stones were sometimes associated with beds of turtle grass (*Phallasia*) and usually with very small growths of coral. On the reefs *H. carunculata* can be found at any time of day in the interstices of the reef and, in the late afternoon, early evening, or early morning many individuals can be seen crawling slowly over the coral. This species does not breed during the summer.

H. carunculata has been reported from the Gulf of Mexico by Hartman (24) and from southern Florida by Mullin (33) and Monro (31). Judging from its abundance in Barbados and Jamaica and its recorded occurrence in Tobago and Grenada, it is presumably to be expected throughout the Caribbean. Hartman (26) says that it is generally associated with drifting objects in warm currents.

Family PHYLLODOCIDAE

EULALIA MYRIACYCLUM (Schmarda), 1861

Notophyllum myriacyclum Schmarda, 1861, 87, Pl. 29, Fig. 233 (41)
Eulalia quinquelineata Treadwell, 1902, 192, Figs. 27–29 (43)
Eulalia myriacyclum Hartman, 1951, 33–34 (26)

One complete specimen was taken from a crevice in coral at Needham Point, Barbados, and another was collected at Quaco Point, Jamaica. Incomplete fragments have frequently been encountered in pieces of coral rock taken from a variety of localities on both islands. It is known from the Caribbean Sea and the eastern part of the Gulf of Mexico.

Phyllodocid larvae were found in the plankton taken off the Barbados coast throughout the summer months. The larvae appear to be of two types. One was found in the plankton in late May as a short, sturdy, translucent larva with six setigerous segments, a pair of large, red eyes, and five prostomial tentacles (Fig. 2). The other type of phyllodocid larva occurred in the plankton in July and August. Two developmental stages of this larva were found. The younger stage was a posttrochophore with 10–14 setigerous segments, a conspicuous, ciliated prototroch, a pair of small, red eyes, four prostomial tentacles, and a mass of dark-green yolk filling the posterior part of the body (Fig. 3). The older stage of this larva had up to 27 setigers, had lost the prototroch, and acquired the adult complement of four pair of peristomial and two pair of prostomial tentacles (Fig. 4). In these older forms the green yolk had become confined to the posterior part of the digestive tract and the head had acquired a more definitive shape and was clearly set off from the rest of the body. Neither of these two types of larvae can be related positively to any one adult phyllodocid species. The second type (with the green yolk) is obviously not *E. myriacyclum* since it has four, not five, prostomial tentacles. The first larval type might possibly be *E. myriacyclum* but there is no conclusive evidence to show this.

Family PILARGIIDAE

ANCISTROSYLLIS sp.

It is most unfortunate that only one incomplete specimen of this rare and interesting family was found. The specimen concerned comes from the Barbados plankton and was taken in a stramin net on the night of June 1, 1956. The available portion of the body was 3 cm long and lacked the posterior extremity.

The Barbados specimen fits the genus *Ancistrosyllis* as described by Hartman (23) in the following respects. The body is elongate and on the prostomium there are three antennae and one pair of biarticulated palpi. The proboscis is cylindrical, muscular, and lacks jaws (Fig. 5). The peristomium bears cirri (probably two pair, Fig. 7). Both neuro- and noto-setae are present and the neurosetae are whorled (Fig. 6). There are furcate setae in the neuropodium (Fig. 8) and acicular spines in the notopodium (Fig. 6).

On the other hand, this specimen is unlike *Ancistrosyllis* and other Pilargiidae in lacking a toothed cutting edge on the neurosetae (Fig. 8). The Barbados specimen is also unusual in the nature of the tall papillae at the distal end of the pharynx (Fig. 5) and in the presence of foliaceous gills on the dorsal and ventral surfaces of the first 15 segments (Fig. 6). Two other special aspects of this animal which are probably related to its pelagic habit are the very large prostomial eyes and the eyespot on the posterior margin of each parapodium. It is in fact not unlikely that this planktonic form is a late larval stage of some so far unidentified adult pilargiid. Certainly further representatives of this family will be looked for in Barbados with interest.

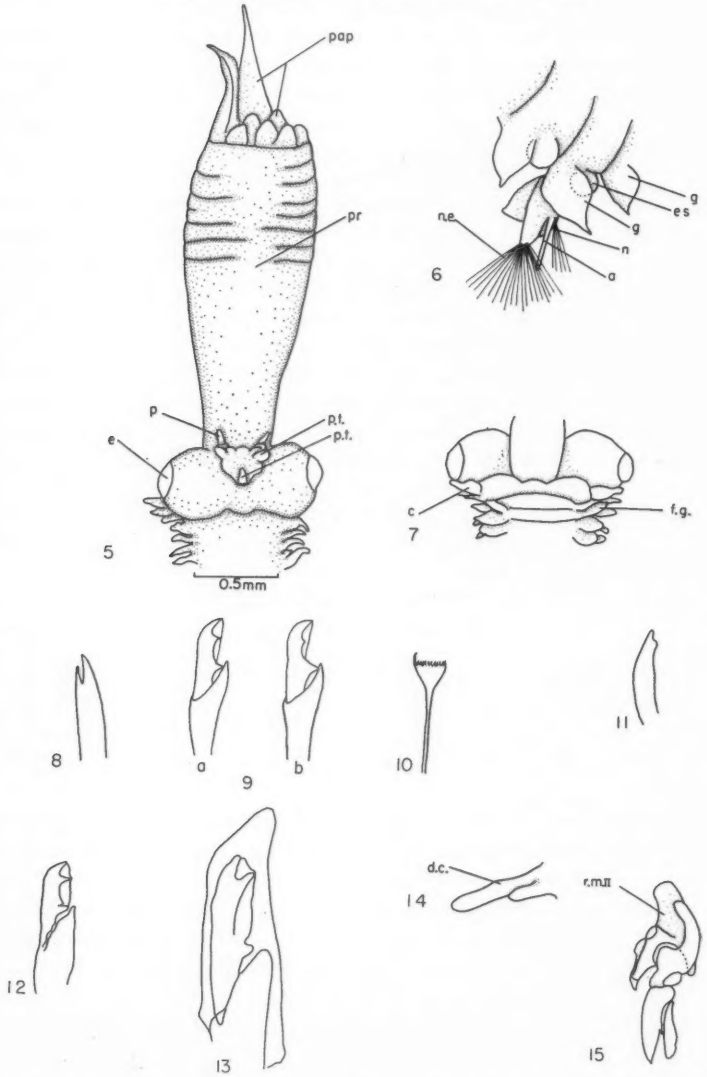


FIG. 5. *Ancistrosyllis* sp. A dorsal view of the anterior end of the body. FIG. 6. *Ancistrosyllis* sp. Fourth segment and appendage. Dorsal aspect. FIG. 7. *Ancistrosyllis* sp. Ventral view of the anterior end. FIG. 8. *Ancistrosyllis* sp. Neuropodial setae.

FIG. 9. *Eunice tridentata*. Compound setae, (*a*) with large accessory tooth, (*b*) with small accessory tooth. FIG. 10. *Eunice tridentata*. Pectinate setae. FIG. 11. *Eunice tridentata*. Subacicular hook. FIG. 12. *Eunice mutilata*. Compound seta. FIG. 13. *Eunice aphroditois*. Compound neuropodial seta.

FIG. 14. *Palola siciliensis*. First parapodium. FIG. 15. *Palola siciliensis*. Jaws on right side.

ABBREVIATIONS: a = aciculum, c = cirrus, d.c. = dorsal cirrus, e = eye, es = eyespot, f.g. = first gill, g = gill, n = notoseta, ne = neuroseta, p = palp, pap = papilla, pe = peristomial eye, pr = proboscis, p.t. = prostomial tentacle, r.m.II = right maxilla II.

Family SYLLIDAE

TYPOSYLLIS CORALLICOIDES Augener, 1922

Syllis (Typosyllis) corallicoides Augener, 1922, 42–43 (2)
Typosyllis corallicoides Hartman, 1951, 41–42 (26)

Five specimens come from Paynes Bay, Barbados. This species was formerly known from Mexico (Veracruz) and Florida (Tortugas) as well as the West Indies.

The body appears to consist of three regions. The most anterior is about 16 segments long, rather wide, and slightly compressed dorsoventrally. Behind this is a region in which segments become progressively longer. At about the 65th or 70th they reach their maximum length and then become progressively shorter. At the posterior end of the body the segments are short and crowded. It is in this region that epitokes arise.

ODONTOSYLLIS ENOPLA Verrill, 1900

Odontosyllis enopla Verrill, 1900, 603–604 (50); Hartman, 1951, 41 (24)

Four individuals, all gravid females and none complete in one piece were taken by A. G. Fish from the surface water in the lagoon at Sandacres, Barbados, on the night of June 26, 1959. At the time of collection the worms were luminescent and were exuding a luminescent material, probably in relation to their typical spawning behavior as described by Galloway and Welch (19) and Huntsman (28).

Family NEREIDAE

NEREIS RIISEI Grube, 1856

Nereis riisei Grube, 1856, 162–163 (20)
Nereis ambiguens Treadwell 1937, 149–151, Pl. 2, Figs. 19–24 (49)

Four specimens were taken from the lagoon at Sandacres, Barbados, on the night of June 20, 1957, using a night light. The largest specimen was 8 mm long. All showed some degree of epitoke development at the posterior end of the body but none were completely mature. A single specimen of this species was taken at Six Men's Bay, Barbados, in May, 1955, and another at Portland Point, Jamaica, in August, 1954.

This species is known from both sides of tropical and temperate America including Mexico and the Florida Keys and the southern part of the Gulf of Mexico.

PERINEREIS ANDERSSONI Kinberg, 1886

Nereis bairdii Webster, 1884, 312–313, Pl. 8, Figs. 22–28 (51)
Perinereis anderssoni Hartman 1948, 72–73 (with synonymy) (25)

Two specimens were taken at Six Men's Bay, Barbados, on July 8, 1955, and one from Bathsheba, Barbados, on May 12, 1955. Of these, two were

about 30 mm long and one was about 15 mm long. The body is a brilliant turquoise color fading to white anteriorly. One of the larger specimens, collected in May, had the body cavity filled with loose, white ova.

This species is common in Bermuda, the West Indies, and south to Brazil.

NEREIS PELAGICA OCCIDENTALIS Hartman, 1945

Nereis pelagica occidentalis Hartman, 1945, 20, Pl. 4, Figs. 1–6 (24)

Three specimens were taken at Six Men's Bay, Barbados, on July 8, 1955. One was a female carrying ova in the body cavity. This species is known from North Carolina, southwest Florida, and Louisiana.

Family EUNICIDEA

EUNICE TRIDENTATA Ehlers, 1905

Eunice tridentata Ehlers, 1905, 288, Pl. 9, Figs. 3–10 (11); Augener, 1924, 402–404, Fig. 8 (3); Monro, 1933, 63–64, Fig. 26 (31); Hartman, 1944, 114–115, Pl. 7, Figs. 145–150 (23)

Leodice valens Chamberlin, 1919, 257–258, Pl. 1, Figs. 6–8 (7)

This species was collected from fragments of coral at Sandacres, Barbados, on July 18, 1955. One complete individual was found along with two fragments from the mid-body region of other individuals.

The specimens from Barbados are in most respects more like the type material (11 and 3) than they are like the Californian worms described by Hartman (23). With regard to the subacicular hooks, however, the Barbados material resembles Hartman's description more closely. The diagnostic features of the Barbados material are as follows: heavy branchiae are present from the sixth parapodium back. The maximum number of filaments per gill (11) was found on the 16th parapodium. On the 72nd there was only a single filament and branchiae were absent from the 76th parapodium to the posterior extremity. The compound setae bore a tapering distal fang and an accessory tooth which varied from very small (Fig. 9*b*), as in Hartman's material (23) to rather heavy (Fig. 9*a*), as in Ehlers (11) specimens. The guard at the base of the appendage, when unworn, resembles a third tooth (Fig. 12). Pectinate setae are present in the dorsal part of the fascicle from at least the 10th segment back. The dentate edge is nearly straight and bears a large tooth at one end (Fig. 10). Acicula are black, curved, and tapered distally. Subacicular hooks are dark, heavy, and distally bifurcate. In the Barbados material the secondary tooth is the smaller (Fig. 11) as it is in Hartman's (21) description. In the type material the secondary tooth is the larger. Maxilla II has four to five teeth on the left side as compared with three to four in the type material.

Previous records for this species place it on the Pacific coast of America from Panama north to Lower California. This is the first time it has been recorded from the Caribbean.

EUNICE MUTILATA Webster, 1884

Eunice mutilata Webster, 1884, 315–316, Pl. 9, Figs. 36–40 (51); Hartman, 1944, 113–114, Pl. 6, Figs. 140–141 (23)
Eunice barvicensis McIntosh, 1885, 292–294, Pl. 39, Fig. 12, Pl. 21*a*, Figs. 1–3 (30)
Leodice mutilata Treadwell, 1921, 30–33, Pl. 3, Figs. 5–8, Figs. 66–67 (46)
Eunice afra Monro, 1933, 66–67 (31)

One complete individual and anterior portions of five others were collected from coral fragments at Speightstown, Barbados, on May 21, 1955.

When alive the animals were purplish brown in color at the anterior end, becoming greenish behind. The dorsal surface in the anterior region tended to be finely reticulated. The middle region of the body, in one specimen, was marked dorsally with many pale, round spots. The anterior borders of the ventral lips, the tips of the prostomial cirri, and all the peristomial cirri were white. The fourth parapodial segment was pigmented in its anterior half, white in its posterior half. The complete individual was 24 cm long and the six individuals concerned in this collection were found in one fragment of coral of about 6 cubic inches.

Branchiae begin on the 5th or 6th parapodium as a single filament and the number increases to a maximum of 17 filaments on the 28th parapodium. The number of filaments remains high back to about the 40th segment. Posterior to this region the gills become smaller with fewer filaments and eventually disappear about 25 segments from the posterior end of the animal. Acicula are black. There are two per parapodium in the more anterior region of the body (segments 15 and 56 examined) and one per parapodium farther back (segment 100 examined). Subacicular hooks are dark; they appear first at about the 28th segment and are distally tridentate. The composite setae are pale and distally bidentate. The hood over the appendage appears to have a delicately dentate edge (Fig. 12).

This species has been reported from Bermuda, the West Indies, the Dry Tortugas, and the eastern Pacific, from the shore to 18 fathoms.

EUNICE APHRODITOIS (Pallas) 1766

Eunice aphroditois Fauvel, 1917, 215–225, Pl. 7, Fig. 18 (13); Monro, 1933, 58–59 (31); Hartman, 1944, 109–110 (23)

A single, incomplete specimen received from the collection in the Barbados Museum is tentatively assigned to this species. It was collected by Mr. Webster near Animal Flower Cave, Barbados, at some unspecified time prior to 1955. The specimen is large, 3 ft long, although incomplete posteriorly, with a maximum diameter of 2 in. When first examined the color had faded to a pearly grey iridescence and the cuticle had started to loosen on the body. The available portion of the animal includes prostomium, peristomium, and 205 setigerous segments. The prostomial and peristomial cirri are short, extending back about two-thirds the length of the peristomium and appear

to be irregularly and indistinctly ringed. The exact nature of the ringing is obscured by the loosening of the cuticle. The peristomium is rather long, equivalent in length to the following five setigerous segments. Branchiae appear first on the 6th setiger as a single, minute filament and reach maximum size on the 15th parapodium where the gill consists of a sturdy stem bearing 45 filaments along one side. Two of the filaments on this gill were divided although in most cases the filaments are all simple and undivided. The branchiae continue to the end of the available portion of the animal, very gradually decreasing in size. On the 205th setiger the gill bore 28 filaments. In this region the body has obviously begun to taper toward the posterior end.

Setae and acicula were all much worn and perhaps softened by improper preservation. Acicula were black with rounded tips except for buried ones which tapered to fine, filament-like points. The number of acicula varied as follows: in the 10th parapodium there were three projecting and two buried acicula; in the 37th parapodium there were five projecting acicula; in the 80th parapodium there were two exposed acicula and one buried; and in the 205th parapodium there were three exposed acicula. The compound neuropodial setae were in most cases very much worn with the distal appendage lost. When present, the appendage was clearly bidentate (Fig. 13). It has been assumed that the subacicular hooks were likewise badly worn since in no case could they be distinguished from the worn compound setae. In some cases the worn ends of such setae were notched in a manner suggestive of the bidentate subacicular hooks characteristic of *E. aphroditois*, but in no case was an unmistakable subacicular hook identified. None of the neuropodial setae (or hooks) were black but varied in shade from pale to very dark amber. Judging from the descriptions of Fauvel (13), Monro (31), and Hartman (23) the subacicular hooks are absent from a progressively longer region, beginning at the anterior end of the body, as the animal increases in size. In the largest specimen recorded, $3\frac{8}{10}$ meters long (13), the subacicular hooks appeared between segments 90 and 100. Opinions on whether or not one should expect subacicular hooks in the incomplete Barbados specimen depend, therefore, on estimates of the probable total length of the animal and, since this is the only specimen of the species ever seen by this author, such an estimate is impossible to make.

In addition to the setae described above the dorsal cirri throughout the body were each supported by a bundle of narrow, black rods completely buried in the flesh at the base of the cirrus. Groups of five, six, and seven rods have been examined. They are much slighter than the acicula, taper more slowly, and end in blunt, yellow tips buried in the flesh. Ova, somewhat sticky and probably not yet mature, were found in the parapodia from the 80th segment back.

This species has a circummundane distribution in the tropics and subtropics and has been reported from the Red Sea, Ceylon, the Philippines, Borneo, Japan, Samoa, Australia, New Zealand, the Maldives, South Africa, the Antilles, and the Mediterranean.

EUNICE RUBRA Grube, 1856

Eunice rubra Ehlers, 1887, 87–88, Figs. 1–11 (9); Hartman, 1944, 117, Pl. 7, Figs. 151–153 (23); Hartman, 1951, 55 (26)
Eunice ornata Andrews, 1891, 284–285, Pl. 13, Figs. 6–13 (1)
Leodice rubra Treadwell, 1921, 15–17, Pl. 2, Figs. 1–4, 13–20 (46)

One specimen, complete except for some damage to the middle region of the body, was collected from the reef at Sandacres in shallow water on July 18, 1955.

Branchiae begin on the second setiger and bear six filaments where these are best developed. About 44 segments are branchiate. Subacicular hooks are pale and distally tridentate and hooded. Compound setae are bidentate and hooded. Acicula are yellow and distally bidentate.

Immature ova were found in the middle region of the body.

This species occurs on the eastern coast of the Americas from North Carolina south to Brazil, including the eastern part of the Gulf of Mexico.

EUNICE SCHEMACEPHALA Schmarda, 1861

Eunice schemacephala Schmarda, 1861, 132, Pl. 2, Fig. 260, seven text figures (41); Hartman, 1944, 121 (23); Hartman, 1951, 56 (26)
Eunice fucata Ehlers, 1887, 91–93, Pl. 25, Figs. 8–20 (9)

Several specimens, one complete, were collected at Hastings, Barbados, from old coral on June 24, 1955.

Branchiae appear first on the sixth parapodium as a single filament. There are two filaments on the 8th parapodium, three on the 10th to 17th, and then the number decreases posteriorly. The last gill is found on the 87th parapodium as a small, single filament. No more than three filaments were found on any one parapodium in any of the material examined. The number of filaments observed here is smaller than that described by Ehlers (9) but the general distribution of branchiae is similar.

Acicula are dark and there are usually two in a parapodium. Subacicular hooks appear first in the 30th segment. They are dark, end in a single falcate tip, and are usually present singly.

The characteristic swarming behavior of this 'Atlantic Palolo' has not been observed in Barbados.

This species has been reported from the West Indies, the Dry Tortugas, and the Atlantic coast of Panama.

PALOLA SICILIENSIS (Grube), 1840

Eunice leucodon Ehlers, 1901, 128–230, Pl. 6, Figs. 1–10 (10)
Leodice viridis vernalis Treadwell, 1922, 133–134, Pl. 1, Figs. 8–11 (47)
Eunice siciliensis Fauvel, 1923, 405–407, Fig. 159 (14). Monro 1933, 62 (31)
Palola siciliensis Hartman, 1944, 131 (23); Rioja, 1946, 194 (40); Hartman, 1954, 621, Fig. 169D (27)

Three individuals, all incomplete posteriorly, were collected at Speightstown, Barbados, on May 21, 1955, in pieces of old coral. The largest individual consisted of about 140 segments.

Branchiae are limited to the posterior region of the body, appearing first on the 105th segment. The single aciculum is dark and blunt. The notopodial setae are simple, curved, and toothed; the compound neuropodial setae are tridentate. The first parapodium bears no setae and carries a very long dorsal cirrus (Fig. 14). Maxilla II on the right side bears two definite, if rounded, denticles and one proximally placed, rather indeterminate lump (Fig. 15).

The distinction between this species and *P. paloloides* (33) appears to be rather unsatisfactory. According to Hartman (23) the differences are small and concern longer cirri on the first parapodium in *siciliensis* and three, rather than two, denticles on the right maxilla II in *paloloides*. On the other hand, the maxillae of *siciliensis* later figured by Hartman (27) show three distinct teeth on the right maxilla II. In fact these teeth figured for *siciliensis* are far more distinct than those shown for *P. pallidus* (21), later synonymized with *P. paloloides*. In the Barbados specimens the blunt irregularities on the right maxilla II (Fig. 15) could easily be interpreted as three teeth or as two with a lump and it seems clear that the number of teeth on maxilla II is not a satisfactory means of distinguishing between the two species *paloloides* and *siciliensis*. The only remaining diagnostic feature is therefore the length of the cirri on the first parapodium and it seems that the question of the validity of these two species deserves some study.

This species is found in tropical regions around the globe.

Family ARABELLIDAE

ARABELLA IRICOLOR (Montagu), 1804

Arabella iricolor Fauvel, 1923, 114 (15); Hartman, 1944, 257 (23)

Six complete specimens were taken from cavities in coral rock on sand in 6 feet of water at Sandacres, Barbados, on July 22, 1955.

In the life the body has a pinkish iridescence with the red blood vessels showing clearly, especially in the parapodia.

This species has a cosmopolitan distribution in temperate and tropical seas.

Family SPIONIDAE

DISPIO UNCINATA Hartman, 1951 ?

Dispio uncinata Hartman, 1951, 86–90, Pl. 22, Figs. 1–5, Pl. 23, Figs. 1–4 (26)

A single specimen, about 9 cm long, was taken at Sandacres, Barbados, on August 9, 1957, from a burrow in sand in about 6 feet of water.

This one specimen, an ovigerous female, is rather like, but does not entirely fit, the description of the new genus *Dispio*, described by Hartman (26). It resembles *Dispio*, rather than *Spio*, in having accessory branchiae (Fig. 16) on the middle and posterior portions of the body, but differs from *Dispio* in that the first few notopodial lobes are not distinctly serrated. The first three

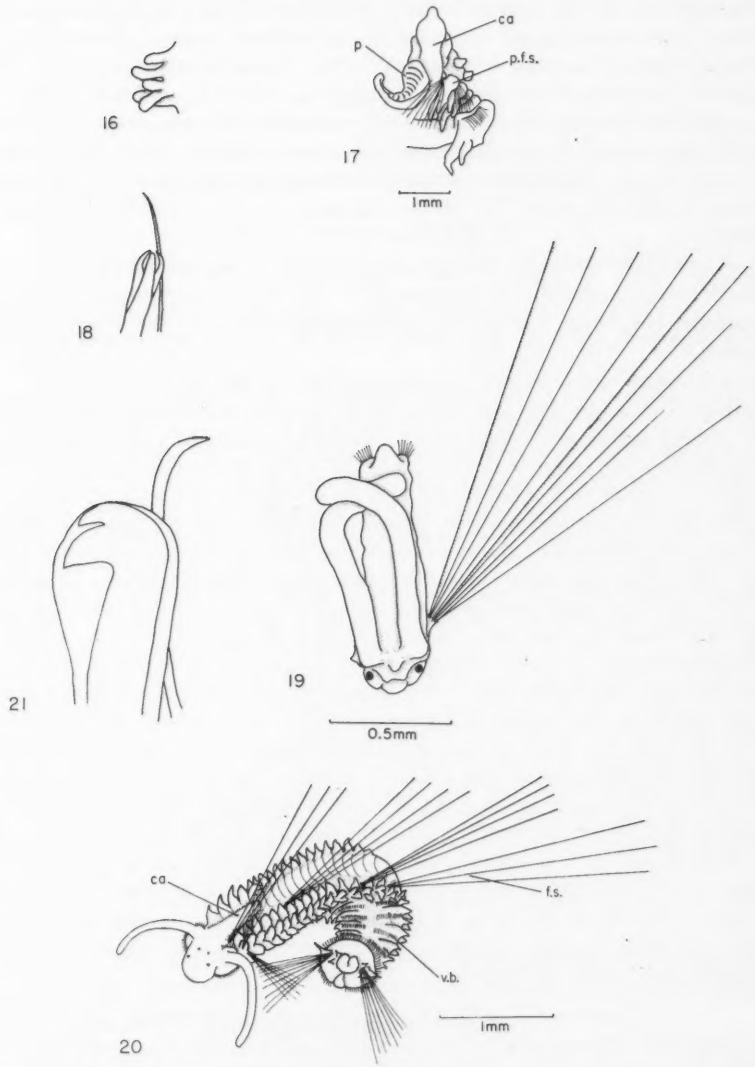


FIG. 16. *Dispio uncinata* (?). Accessory branchiae.
FIG. 17. *Dispio uncinata* (?). Dorsal view of the anterior end, one palp lost.
FIG. 18. *Dispio uncinata* (?). Neuropodial setae, a hooded hook and accompanying seta from the posterior region of the body.
FIG. 19. Young spionid larva with one pair of bundles of long setae.
FIG. 20. Older spionid larva, beginning to lose flotation setae.
FIG. 21. Older spionid larva. Neuropodial setae from one of the four last segments of the body.

ABBREVIATIONS: ca = caruncle, f.s. = flotation setae, p = palp, p.f.s. = parapodium of first setiger, v.b. = ventral brush of cilia.

notopodial lobes in the Barbados specimen are set off from the following notopodia by their small size, but they do not exhibit conspicuous serration.

The general appearance of the head of the Barbados specimen (Fig. 17), including the prostomium, size and shape of the caruncle, and the position of the palpi is very much like that of *Dispio uncinata* Hartman (26). There are apparently no eyes in the Barbados specimen although they may possibly remain hidden in the folds of the head formed during fixation. The nature and arrangement of the setae (Fig. 18) are similar in *D. uncinata* and the Barbados specimen.

It is obviously desirable that more specimens of this species be found and studied before a definite identification of the Barbados material is made. At present the single specimen is assigned tentatively to the species *Dispio uncinata*.

In life the animal is a dark-red color and the ova are white.

Spionid larvae are abundant in the Barbados plankton throughout the summer. Young larvae with one or more pairs of bundles of very long, barbed setae (Fig. 19) are common in the months of May and June and tend to be less numerous in July and August. At this time older larvae with an increased number of segments and many bundles of long setae (Fig. 20) begin to appear. A conspicuous feature of these larvae is the series of thickly ciliated ventral bands (Fig. 20). Such older stages have been kept in the laboratory for as long as 3 weeks. They tend to settle at the bottom of the container and to lose the long setae which are clearly a flotation device characteristic of the younger, planktonic stages. At the time of settling the larva has bundles of simple, limbate, notopodial setae and a few groups of hooded hooks and associated simple setae on the posterior neuropodia (Fig. 21). Whenever these older larvae were placed in water above sand they immediately began to burrow, head first. As the animal disappears from sight the opening of the burrow becomes marked by a small cone of sand. Frequently the tentacles of the occupant can be seen protruding from the burrow. In the younger larvae the gut is filled with yellow-brown yolk. In the older larvae the color of the gut fades and the tentacular palps, previously transparent, become a faint red.

The abundance of this larva throughout the summer suggests that it may belong to some common species of spionid but there is as yet no means of identifying the adult concerned.

Family MAGELONIDAE

Magelonid larvae are common in the Barbados plankton in the summer months of June and July. The largest planktonic forms seen were 10 mm long and quite transparent except for four small, red eyes, some red and white pigment at the tips of the tentacles, and a little yellow color at the posterior end of the gut.

None of the larvae examined were old enough to make specific identification possible, due largely to the absence of parapodial lobes of any sort. The genus is probably *Magelona* as there are frontal horns on the prostomium. The

first nine segments bear long, limbate, slightly curved setae and the ninth setiger does not appear to carry special setae. In the posterior region of the body there are hooded hooks situated both ventrally and dorsally in each segment. The hooks each carry a terminal fang and two transversely arranged teeth. The types and disposition of the setae are suggestive of *Magelona japonica* (36) but the complete absence of parapodial lobes in these larval forms makes it impossible to make a definite identification.

Family CHAETOPTERIDAE

CHAETOPTERUS VARIOPEDATUS (Renier), 1804

Chaetopterus pergamentaceous Leidy, 1888, 73–74 (29)
Chaetopterus variopedatus Fauvel, 1927, 77–79, Fig. 26 (16); Hartman, 1945, 34–35 (24)

Chaetopterus variopedatus was collected in Jamaica at Kingston Harbour by Mr. D. Erdman in 1953 and again at Old Harbour Bay in 1954. The first specimen, taken in June, was an ovigerous female and came from black mud in 2–3 fathoms of water. The second came from muddy sand in about 3 feet of water, very close to shore. This species has also been reported from Puerto Rico and Florida. Its distribution is cosmopolitan and it is certainly to be expected in Barbados.

This family is represented in the Barbados collection, however, by a larval form only. The larva is common in the plankton from early July until late in August, being most abundant in late July.

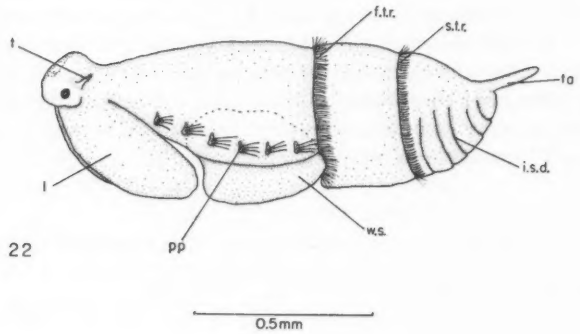
The youngest chaetopterid larvae found in the plankton appear as plump trochophores or posttrochophores, colored green and bearing two complete trochal rings of cilia (Fig. 22). The mouth is very large and is bordered ventrally and laterally by a pair of thick, white lips. Dorsally the head bears a pair of tentacle rudiments and anterior to the base of each tentacle is a bright-red eye. On the dorsal surface of the head, between the eyes, is a pattern of dark-red spots. A thin line of dark-green pigment extends from the ventral side of the head forward between the two lobes of the lip.

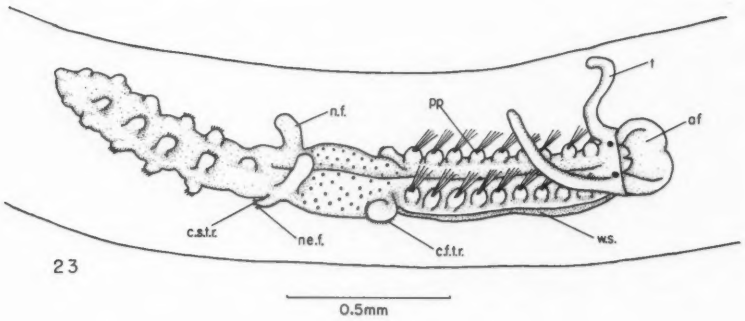
Behind the head the interior of the body is a bright green due to endodermal masses of granular yolk.

At the posterior end of the body is a small, translucent, tail-like projection. The 'tail' is very extensible and secretes a sticky material by means of which the larva may anchor itself temporarily to the glass of the container.

Between the head and the anterior trochal ring develop the rudiments of the parapodia. In some of the young larvae six segments have been seen in this region. Median and ventral to the paired parapodial rudiments is an area of smooth, white material. It may appear as a white lump lying behind the lips and in front of the anterior trochal ring. The region between the trochal rings does not appear to give rise to segments.

Behind the posterior trochal ring the ventral region of the body forms a convex curve and bears the marks of intersegmental depressions. From three to six such depressions have been seen in the young larva. The ventral region





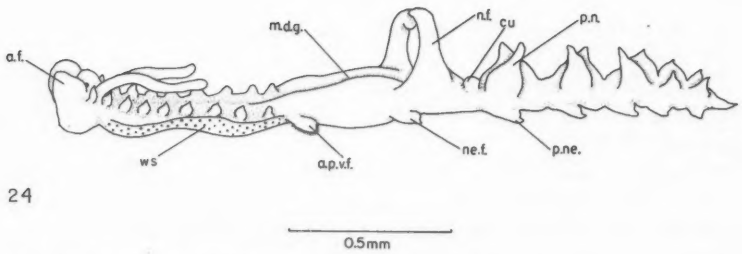


FIG. 22. Young chaetopterid larva, from the plankton.
FIG. 23. Older chaetopterid larva.
FIG. 24. Tubiculous chaetopterid larva.

ABBREVIATIONS: a.f. = anterior fold, a.p.v.f. = anterior pair of ventral flaps, c.f.t.r. = cilia of first trochal ring, c.s.t.r. = cilia of second trochal ring, cu = cupule, d.f. = dorsal flap, f.t.r. = first trochal ring, i.s.d. = intersegmental depression, l = lip, m.d.g. = middorsal groove, n.f. = notopodial flaps, ne.f. = neuropodial flaps, p.n. = posterior notopodia, p.ne. = posterior neuropodia, pp = parapodia, s.t.r. = second trochal ring, t = tentacle, ta = "tail", w.s. = white shield.

is also marked by a deep groove in the mid-line, dividing the segmental ridges into right and left parts. The 'tail' lies at the point where the convex ventral surface meets the much shorter, flatter, dorsal surface. The 'tail', therefore, is dorsal in position (Fig. 22).

Larvae at this stage when kept in the laboratory tend to secrete considerable quantities of mucus and although they tend to spend most of their time at mid-water levels they are frequently surrounded by a thin mucus halo. In some cases several larvae may remain more or less permanently associated with one another in a common mass of mucus. This presumably does not occur in the plankton, and freshly caught larvae have never been found encumbered in this fashion.

In somewhat older larvae (Fig. 23) the body has elongated. The paired lip lobes have come to extend forward in front of the head and in this position they fuse to form a bilobed ridge or fold of tissue. Ventrally this lobe appears to be continuous with an area of opaque, white tissue which extends back to the anterior trochal ring forming a shield-like structure between and ventral to the paired rows of parapodia. There are nine pair of parapodia each taking the form of a single bulb bearing a tuft of fine setae. The first trochal ring is now incomplete dorsally and has extended laterally onto a pair of small, flap-like appendages. The tentacles have become longer.

The intertrochal region, still without parapodia, is short. Within it the digestive tract is filled with granular masses of green yolk. Anterior to the first trochal ring the digestive tract, an apparently straight tube, is colorless and contains no yolk.

Behind the second trochal ring the body has become longer and the ventral surface is not markedly convex. The second trochal is likewise incomplete dorsally. The body behind the second trochal ring is divided into five rough segmental units and each unit bears two pair of lateral, apparently ciliated projections. The "tail" has become reduced to a short stump and the anus opens ventrally at its base. The intestine usually includes one simple coil near its posterior end and is filled with bright-green yolk granules. At the level of the second trochal ring there are a pair of small, lateral projections covered with cilia and also a pair of larger, unciliated dorsal flaps. Behind these structures, in the middorsal line, there is a small lump.

At this stage the larva tends to crawl on the bottom, frequently forming a deposit of slime which will harden if not disturbed. In one case the slime deposit took the form of a tube attached to the glass, entirely enclosing the animal. This individual was observed for 10 days before it died.

Eight to 10 days after the formation of the tube the animal had become somewhat longer and more slender (Fig. 24). The anterior bilobed fold had shortened and now curved dorsally on either side of the head. The tentacles were smaller and shorter and behind the head the nine pair of parapodia had come to occupy a diagonal position, the anterior pair being dorsal, the posterior pair ventral. A deep middorsal groove developed between the two rows of parapodia. The ventral surface of the body in this region was covered by a

shield of opaque, white material. Immediately behind the ninth pair of parapodia was the ventral pair of small, flap-like appendages edged with conspicuous cilia, the only trace of the anterior trochal ring. Behind these appendages was a mid-body region, opaque white and granular in appearance. At the posterior limit of the mid-body region were two pair of lobes, representing probably, the neuro- and noto-podia of a single pair of parapodia. The neuropodia were short, rounded, and ciliated, the notopodia tall, tapering, and flexible and located on each side of the deepest part of the middorsal groove. Immediately behind this pair of parapodia was the small, rounded, median projection, presumably the rudiment of the cupule. The body behind the cupule bore the rudiments of five pair of appendages, the neuropodia short, rounded, and ciliated, the notopodia taller, triangular, and decreasing in size toward the posterior end of the body.

At this stage the larva lay on its ventral side in the tube. It moved frequently, often doubling on itself as it changed direction. The body as a whole pulsated constantly and a current of water was continuously drawn into and through the tube.

It was not possible to raise these larvae to an age at which the species could be determined.

Family PECTINARIIDAE

PECTINARIA CHILENSIS (Nilsson), 1928

Pectinaria (*Cistenides*) *chilensis* Nilsson, 1928, 37–40, Figs. 11A–11G (35); Hartman, 1940, 333, Pl. 50, Figs. 12 and 15, Pl. 51, Fig. 19 (22)

Four animals and three complete tubes were collected at Sandacres, Barbados, on August 5 and 12, 1955. They were found under stones near the water line on the sand beach. Empty tubes have frequently been found on the sand in deeper water at the same location.

The Barbados specimens fit the description for this species as given by Hartman (22) very well except for the color of the tube, which is neither white nor greyish but a mosaic of sand grains ranging in color from golden brown to white.

This species was previously known from Chile and Peru. This is the first record from the Atlantic side of the Americas.

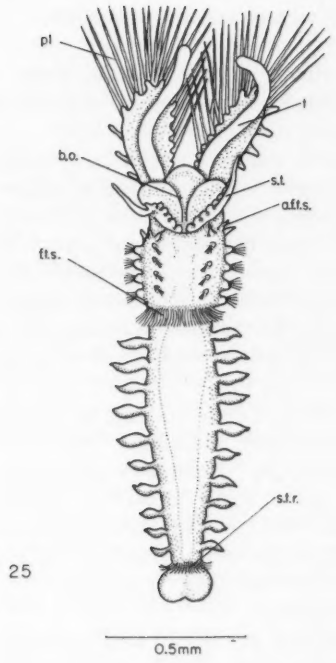
Family SABELLARIIDAE

PHRAGMATOPOMA CALIFORNICA (Fewkes), 1889

Sabellaria californica Fewkes, 1889, 113–132, Pl. 7, Figs. 3, 4 (18). Moore, 1909, 293–294, Fig. 6 (33); Treadwell, 1914, 227 (44); Chamberlin, 1918, 180 (6); Chamberlin, 1919, 261 (7); Berkeley, 1941, 50 (5)

Phragmatopoma californica Hartman, 1944, 249–250, Pl. 29, Figs. 15–17, Pl. 37, Figs. 86–89, Pl. 41, Fig. 105 (23)

Six specimens were taken at Bathsheba, Barbados, on May 11, 1955. The worms inhabit sandy tubes which form aggregations on rocky ledges and



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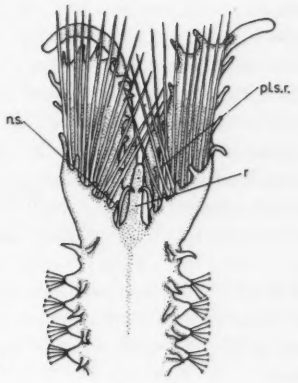

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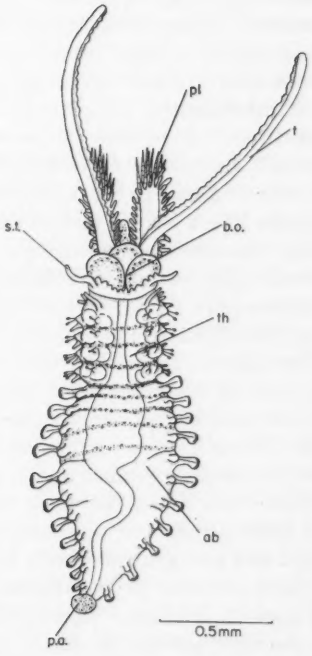

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FIG. 25. Sabellariid larva from the plankton, ventral view.
FIG. 26. Sabellariid larva from the plankton, dorsal view of anterior end.
FIG. 27. Sabellariid larva taken from tube built 10 days earlier.

ABBREVIATIONS: a.t.r. = anterior trochal ring, ab = abdomen, ap.f.t.s. = appendages of first thoracic segment, b.o. = building organ, n.s. = nuchal spines, p.a. = post abdomen, pl = palae, pl.s.r. = palae of second row, r = rostrum, s.t. = small tentacles, t = tentacles, th = thorax.

cliffs at about low water level. Similar aggregations of tubes have been seen at River Bay and Conset Bay, Barbados. They are normally associated with the vermetid, *Spiroglyphus irregularis*.

The animals examined all fit the description for this species as given by Hartman (21). Previously it had been recorded only from the Pacific Coast, from California south to Lower California.

Phragmatopoma californica in Barbados is mature in the late summer (July and August). The ova are white and easily fertilized in the laboratory. The embryos begin to swim when about 16 hours old and by 24 hours they are typical sabellariid trochophores with the characteristic paired set of long bristles, a head fold, a lip fold, an apical tuft, a prototroch, a telotroch, and a pair of small, red eyes, much as described by Wilson (52) for the larvae of British Sabellaria. These larvae did not develop beyond the stage of five large setae in each setal sac and none survived in a normal condition beyond 36 hours.

Older sabellariid larvae were common in the plankton in August and early September. When these larvae are compared with the stages described by Wilson (52) it is apparent that most of them must have been recent metamorphs ready to give up pelagic life and settle to the bottom. A very few, which unfortunately did not survive long, still had the setal sacs and associated palae directed posteriorly. In these individuals the body behind the setal sacs appeared to consist of three segments and a terminal bulb. None of these forms survived long enough for a detailed examination.

Figure 25 is a ventral view of one of the older of the newly caught planktonic larvae. The two trochal rings are still present although thorax and abdomen are now quite distinct, the abdomen ending in a darkly pigmented bulb. The setal sacs have turned forward and now contain well-formed palae held by a fringed membrane. There is a pair of long extensible tentacles, the precursors of the palpi of the adult, and, posterior to the large, ventral mouth parts, is a pair of small tentacles, connected ventrally by a series of small projections which are probably the forerunners of the ventral tentacles of the adult. There are four biramous, thoracic segments presumably representing four parathoracic segments. On each segment the notopodium bears a group of three very fine setae while the neuropodium supports four larger setae. The anterior thoracic segments are probably represented by the three (two dorsal and one ventral) short, tentacular structures situated on each side of the body between the parathoracic region and the mouth parts.

Figure 26 is a dorsal view of the anterior end of the larva shown in Fig. 25. On the right side in the dorsal view can be seen a second row of palae, lying above and across an inner row. The presence of two rows of palae is characteristic of these larvae at about this stage. The dorsal view a so shows a pair of stout, curved spines on either side of a middorsal rostrum at the anterior end of the body. The abdominal region is represented by 10 pair of appendages and a terminal bulb, separated from the last pair of appendages by the telotroch.

Larvae at the stage described above, when placed on a layer of sand, will each build a tube of cemented sand grains. Several larvae have been observed to build tubes, about 3 mm long (much longer than the body) in 10 minutes or less. Others took longer. It was observed, however, that a larva which did not become well started on its tube in the first 10 or 15 minutes usually eventually failed to construct a satisfactory tube. When building a tube the larva picks up sand grains, one at a time, on the tentacles. The sand adheres to the tentacle and appears to be carried back toward the mouth on thin mucus moved by cilia on the surface of the tentacle. In the selection of sand grains the tip of the tentacle may probe considerably below the surface of the sand in the container.

At the base of the tentacles are the three glandular pads which form the building organ. Sand grains are held between the pads and turned slowly. The sandy tube is built first around the middle region of the body where a mucus tube has previously been laid down. Once the tube is started new grains are added only at its anterior end. They are fitted and pushed into place by the building organ, the thorax twisting and turning as necessary, and the abdomen performing continuous pulsing movements. As described by Wilson (52) for the Plymouth larvae many of the sand grains passed to the building organ may not be used, and discarded grains accumulate in a heap beneath the animal. As the tube is built the larva moves forward, eventually constructing a tube which is at least twice as long as its own body. The tube is always curved or sinuous. When several larvae building tubes are kept in one container, the tubes are usually found to be adjacent to or on top of one another.

Figure 27 is a ventral view of the oldest larva studied, an animal taken from a tube it had built 10 days earlier. The tentacles have become slimmer and more delicate and the palae are now in two compact packages. Individual palae are now striated and the edges of the tissue holding them in place are now drawn out into fairly long tentacles. The bases of the thoracic parapodia are packed with a dense, white, granular material. The notopodial setae have expanded, paddle-like tips and there are two in each of the first two parapodia and three in each of the last two. Neuropodial setae are smaller, limbate, and there are three to a parapodium. Each abdominal notopodium bears a row of small, blunt uncini and an internal aciculum. In the abdomen neuropodia are much smaller than the notopodia. The postabdomen or cauda has appeared as a short, dark projection from the posterior end of the abdomen. These larvae were patterned with dark-brown stripes situated ventrally and laterally between the segments of the thoracic region and the anterior part of the abdomen. White pigment tended to accumulate on the tissue sheathing the palae and orange spots were present along the sides of the sheath and the length of the palpi. The dorsal rostrum was white with an orange tip and there were dark-brown spots on the building organ and along the sides of the postabdomen.

The coincidence between the breeding season of *Phragmatopoma californica* and the appearance of sabellariid larvae in the plankton suggests a relationship between the two. However, the presence of the dorsal hooks (Fig. 26)

(nuchal hooks ?) in the larva throws some doubt on this possibility since such hooks are absent from the adult *P. californica*. In order to decide this question it will be necessary to maintain the metamorphosed larvae to a stage at which they can be identified as species.

Family TEREBELLIDAE

LOIMIA MEDUSA (Savigny), 1818

Loimia turgida Andrews, 1891, 293, Figs. 46–49 (1); Hartman, 1945, 46, Pl. 10, Figs. 2, 3 (24)

Loimia medusa Hartman, 1951, 111–112 (26)

Four specimens were collected at Six Men's Bay, Barbados, on July 8, 1955. The body, without tentacles, ranged in length from 14 to 18 mm. The animals occurred in tough tubes with adherent small pebbles and were found under stones in 6–9 feet of water. The same species has also been found at Portland Point, Jamaica.

THELEPUS SETOSUS (Quatrefages), 1866

Thelepus setosus Fauvel, 1927, 273, Fig. 95 (16); Monro, 1933, 266 (32); Rioja, 1946, 198 (40); Behre, 1950, 13 (4); Hartman, 1951, 113 (26)

One incomplete specimen consisting of the anterior end and 24 thoracic segments was brought up in a piece of coral rock from 70 feet of water by Mr. Ted Ross at Sandacres, Barbados, on June 14, 1955. Four specimens were taken in Jamaica, one at Portland Point, and three at Drunkenman's Cay.

This species has been reported from the eastern Atlanic, the Red Sea, the Indian Ocean, the Pacific coasts of Australia and Chile, the Dry Tortugas, the Gulf of Mexico, the Falkland Islands, and Antarctica. It has been found in the littoral zone and in dredge hauls from deeper water.

POLYMNIA NEBULOSA (Montagu), 1818

Polymnia nebulosa Fauvel, 1917, 267, Fig. 28 (13) (with synonymy)

One specimen was taken at Sandacres, Barbados, on July 11, 1955, from the underside of a small rock on sand in very shallow water. Ten individuals were collected in Jamaica in June and July of 1953 at Ocho Rios, Don Christopher's Cove, Lime Cay, Big Pelican Cay, Drunkenman's Cay, Maiden Cay, Port Henderson, and Port Antonio.

These specimens ranged from about 5 to 15 cm in length. The body is exceedingly fragile and the animal therefore difficult to collect. It inhabits a tube of loosely cemented sand grains and shell fragments which is usually attached to the underside of a rock and may penetrate some inches into the sand beneath the rock. *P. nebulosa* was typically found in shallow water, 1–6 feet, inshore of coral reefs. The body has a whitish cast over an underlying purple color. The three pair of branching gills are a deep red when suffused with blood. There is a band of red spots around the dorsal margin of the prostomium. Specimens collected on July 1 in Jamaica contained

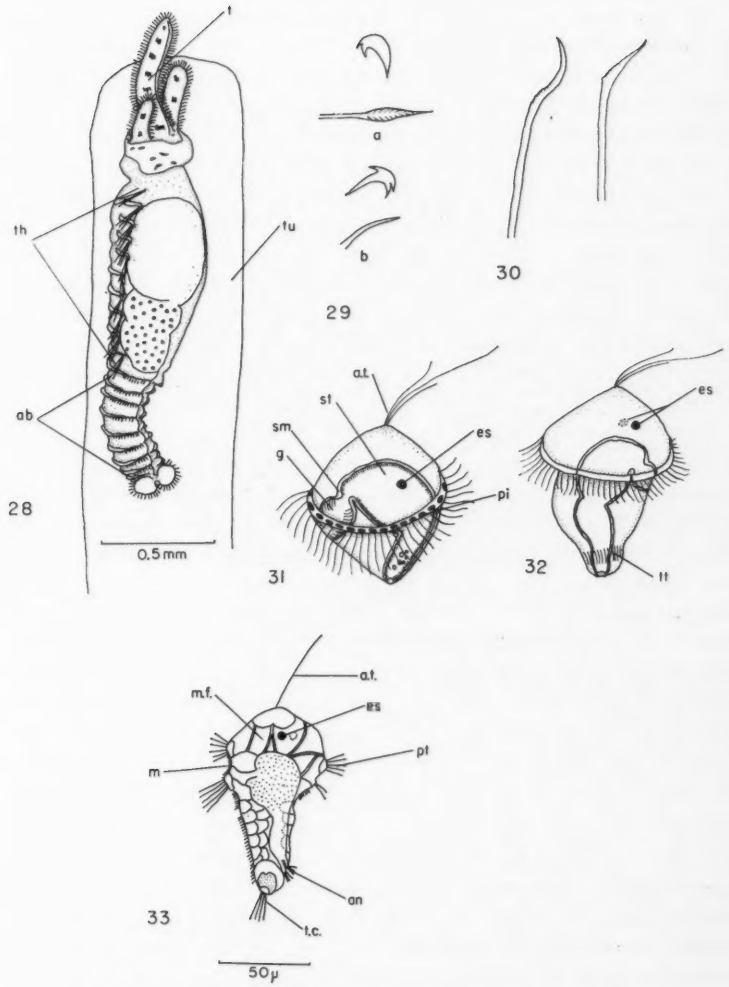

FIG. 28. Terebellid larva in transparent tube. Taken from the plankton.
FIG. 29. Setae from terebellid larva, (*a*) thoracic seta, (*b*) abdominal seta.
FIG. 30. *Spirobranchus giganteus*. Two forms of collar setae.
FIG. 31. *Spirobranchus giganteus*. Trochophore larva 6 days old.
FIG. 32. *Spirobranchus giganteus*. Larva 8 days old.
FIG. 33. *Spirobranchus giganteus*. Larva 15 days old.

ABBREVIATIONS: a.t. = apical tuft, ab = abdomen, an = anus, e.s. = eyespot, g = gullet, m = mouth, m.f. = muscle fibers, pi = pigment, pt = prototroch, s.m. = sphincter muscle, st = stomach, t.c. = terminal cilia, tt = telotroch, th = thorax, tu = tube.

ova in the germinal vesicle stage. The specimen from Barbados, collected on July 11, was kept in sea water in the laboratory and on July 15 spawned large numbers of deep-violet eggs.

This species is known from the North Sea, the Atlantic coast of Europe, the Mediterranean and Adriatic seas, the Indian Ocean, the Persian Gulf, the Pacific coasts of Japan and Australia.

Terebellid larvae were fairly common in the Barbados plankton in June and the first half of July. They all appeared to be of the same type, bearing red-brown spots on the tentacles and black spots on the body. They ranged from a larva about 0.75 mm long with a single tentacle and 6 setigerous segments to others with as many as 7 tentacles, 10 thoracic segments, and 9 abdominal segments. Usually these larvae were found each inside a transparent, cylindrical tube somewhat longer than the body of the larva (Fig. 28). A somewhat older terebellid was taken in a bottle sampler on May 20, 1955. This individual had 12 thoracic and 12 abdominal segments, 14 tentacles and setae as shown in Fig. 29. There were no branchiae.

Unless *Polymnia nebulosa* has a longer and earlier breeding season than is indicated by the limited Barbados and Jamaica collections, it seems unlikely that the larvae common in the plankton belong to this species. At present nothing is known about the breeding seasons of other terebellids in this region.

Family SABELLIDAE

SABELLASTARTE MAGNIFICA (Shaw), 1800

Tubularia magnifica Shaw, 1800, 228–229, Pl. 9, Figs. 1–6 (42)
Bispira melania Mullin, 1923, 52–57, Pl. 1–4 (34)
Sabellastarte magnifica Augener, 1922, 48 (2)
S. indica Rioja, 1946, 198–199 (40)

The four specimens studied in detail come from the reef at Sandacres, Barbados, but this large and easily recognized species is also common at River Bay, Six Men's Bay, Gibbs Bay, and Speightstown, Barbados, and has been collected in Jamaica at Port Henderson, Don Christopher's Cove, Drunkenman's Cay, Port Royal, Montego Bay, Whitehouse Inn, and Scott's Cove. It appears to flourish on boulders and in crevices of stone walls as well as on reefs.

This species is widely known from tropical seas.

HYPSICOMUS ELEGANS (Webster), 1884

Protulides elegans Webster, 1884, 325–326, Pl. 11, Figs. 63–74 (51)
Hypsicomus circumspiciens Ehlers, 1887, 271–277, Pl. 55, Figs. 5–13, Pl. 56, Figs. 1–3 (9); Rioja, 1946, 199 (40)
Sabella alba Treadwell, 1917, 266–267, Pl. 3, Figs. 30–33 (45)
Parasabella sulfurea Treadwell, 1917, 267, Pl. 3, Figs. 30–33 (45)
Hypsicomus purpurens Treadwell, 1924, 20–21, Figs. 30–33 (48)

Hypsicomus phaeotaenia Monro, 1933, 267 (32); Fauvel, 1917, 313–314 (13)
Hypsicomus elegans Hartman, 1951, 115–116 (26)
Sabella phaetaenia Schmarda, 1861, 35, Pl. 22, Fig. 188 (41); Okuda, 1937, 305 (37)

The Barbados collection includes nine specimens from Hastings, three from Six Men's Bay, two from Bathsheba, one from Oistins, five from Sandacres, and three from River Bay. In Jamaica 14 specimens were taken in 1953 and 30 in 1954 at the following localities: Big Pelican Cay, Drunkenman's Cay, Port Henderson, Ocho Rios, Morant Point, Half Moon Bay, Discovery Bay, Port Maria, Maiden Cay, Holland Bay, Quaco Point, and Innes Bay.

Morphologically this is a rather variable species. The Barbados and Jamaica specimens all had eight thoracic segments. Webster (51) describes 6–8 thoracic segments, Fauvel (13) 8, and Ehlers (9) 13. The nature of the setae and uncini in the Barbados and Jamaica material agrees with the descriptions of Webster and Fauvel but Ehler's account does not include the simple capillary setae characteristic of the abdominal region in the Caribbean specimens.

The nature of the collar also seems to vary. In the Barbados and Jamaica specimens the collar lobes were always widely separated dorsally; the collar deeply incised ventrally with a small, double lappet on either side of the midventral line. Monro (32) describes the collar as "entire ventrally" and Fauvel (13) claims that the condition of the collar is variable.

Fauvel (13) describes the color of the branchiae as varying from a dirty white to yellow, red, violet, and brown. Webster (51) describes the pinnae as banded in white and purple. The Barbados forms were always yellow, occasionally spotted or banded with purple. In Jamaica white, yellow, purple spotted, and red forms have been found, although yellow is by far the most common. The base of the tentacular crown, the membrane, is usually purple. The body is basically flesh-colored although the thorax may be marked to a greater or lesser degree with brown or red. The abdomen may have a yellow or greenish tinge.

Worms of this species collected in Barbados and Jamaica in July and August were apparently sexually mature, exuding, when broken either spermatozoa or dark-green ova. Eggs of this species, taken from animals collected at Hastings, Barbados, on August 9, 1955, were artificially fertilized and the embryos reared. Cleavage began at about 2 hours; the first two cleavages were equal, the third unequal and spiral. Between 6 and 7 hours after fertilization the embryos began to swim and at 21 hours they had become trochophores superficially transparent and containing an internal mass of dark-green yolk.

H. elegans occupies channels within rock (coral in the West Indies) and is most common on the older parts of the reef where there is little living coral or on the undersides of loose rocks in the shallow landward of reefs. It appears to prefer dark, well-shaded localities.

This species has been described from Bermuda, the southeastern United States, and the West Indies.

SABELLA MELANOSTIGMA Schmarda, 1861

Sabella melanostigma Schmarda, 1861, 36, Pl. 22, Fig. 190 (41); Ehlers, 1887, 263–266 (9); Monro, 1933*b*, 267 (33); Hartman, 1951, 116–117 (26)

Six specimens were taken at Sandacres, Barbados, on July 11, 1955, and one at Six Men's Bay on May 10 of the same year. *S. melanostigma* was also collected in Jamaica at Portland Point, Port Maria, Don Christopher's Cove, Port Antonio, Montego Bay, Ocho Rios, Lime Cay, and Big Pelican Cay.

This species builds a soft, muddy tube and is usually found in groups anchored to the undersides of rocks, or in deep crevices of rock or reef.

S. melanostigma is common in the West Indies, Bermuda, and the eastern part of the Gulf of Mexico.

MEGALOMMA BIOCULATUM (Ehlers), 1887

Branchiomma bioculatum Ehlers, 1887, 260–263, Pl. 53, Figs. 1–9 (9)
Megalomma bioculatum Rioja, 1946, 199 (40); Hartman, 1951, 115 (26)

Several specimens of this attractive sabellid with branchiae banded in white, orange, and brown, were collected at Sandacres, Barbados, on July 16, 1955. One specimen was preserved immediately and kept; the others were allowed to live in the water table of the laboratory for several weeks and then preserved. This species builds a coarse sand tube which is anchored to the underside of a rock, usually in shallow water.

M. bioculatum is known from Florida, Veracruz, Mexico, and the eastern part of the Gulf of Mexico.

MEGALOMMA LOBIFERUM (Ehlers), 1887

Branchiomma lobiferum Ehlers, 1887, 254–259, Pl. 53, Figs. 10–15 (9); Hartman, 1951, 115 (26)

This species is represented in the Jamaica collection only, and by three specimens, two taken at the Palisadoes, 13-mile post culvert on June 2 and one taken at Innes Bay, August 1, both in 1954. The animals were found in shallow water among mangroves. The branchiae are a purplish red dashed with white in one specimen and orange in the other. The tube is encrusted with large coarse particles.

This species is also known from Key West and Sarasota, Florida.

BRANCHIOMMA NIGROMACULATA (Baird), 1865

Dasychone conspersa Ehlers, 1887, 266–270, Pl. 54, Figs. 1–6 (9); Mullin, 1923, 50–51, Pl. 7, Figs. 1, 2, and 6 (34)
Branchiomma nigromaculata Hartman, 1945, 51 (24); Hartman, 1951, 114–115 (26)

This species is found only in the Jamaica collection but was very common in both coral and mangrove associations and so may be expected to turn up in Barbados. The Jamaica collections include numerous specimens from the

Palisadoes, 13-mile post culvert and from the wall of the swimming pool at Port Royal collected in June and July of 1953 and 1954. There are also four individuals from Retreat Beach taken from the undersides of stones in about 3 ft of water on July 13, 1954 and one from a similar location at Don Christopher's Cove taken on June 9, 1953. The branchiae range in color from a uniform wine red to a background color of red, brown, or tan banded with white.

B. nigromaculata is known to be common in shallow waters in the West Indies, the Bahamas, and south to Brazil on the coast of South America. It also occurs on both eastern and western coasts of Florida.

Branchiomma bairdi (McIntosh), 1885

Dasychone bairdi McIntosh, 1885, 495–497, Pl. 30*a*, Figs. 13–15, Pl. 38*a*, Figs. 5, 6, Pl. 39*a*, Figs. 2 and 9 (30); Augener, 1922, 49 (2); Monro, 1933, 267 (32)

Branchiomma bairdi Hartman, 1951, 115 (26)

This species was found at Oistins and River Bay, Barbados, in 1955 and also at Half Moon Bay, Jamaica, where four specimens were taken from a bed of turtle grass in shallow water on August 13, 1954. The tubes are soft, grey and muddy.

This species is well known from the West Indies and Bermuda.

Family SERPULIDAE

Spirobranchus giganteus (Pallas), 1766

Spirobranchus giganteus Ehlers, 1887, 286, Pl. 67, Figs. 1–7 (9); Fauvel, 1932, 244 (synonymy) (17); Hartman, 1954, 623, 626, 627, and 629 (27)

This long-known and much-debated species has been discussed in some detail by Fauvel (15) in relation to other species of the genus. The following characteristics, cited by Fauvel, have been found to be applicable to the Barbados populations. The collar setae are bayonet-shaped and covered with fine, hair-like processes; the pedicle of the operculum bears a pair of broad, lateral wings; the uncini of the thorax have many teeth and the anterior one is undercut; the uncinigerous tori of the two sides of the thorax are widely separated ventrally in the anterior region and approach each other gradually in the posterior region, thus leaving a triangular depression on the ventral surface of the thorax; the abdominal setae are trumpet-shaped with one distal edge drawn out to a fine point. The features cited above are generic characteristics and in addition in this species the opercular plate is variable in shape and bears two processes which may be branched close to the base; the tube bears three high, serrate ridges, the central ridge ending in a point overlapping the tube opening. To these specific features Pixel (39) adds the dimensions of the abdomen, the length being at least 11 times its greatest breadth. This last feature cannot be applied to any of the populations from Barbados.

The Barbados specimens fall into two categories: (1) a large type which occurs singly, usually on living coral heads, occasionally on old coral rock and (2) a smaller form occurring in dense masses of many tubes cemented together and usually found as an encrustation on rocks at or below low tide level. Apart from this difference in growth habits the two forms appear to be identical morphologically, although within each type there is some variation in the number and form of the collar setae (Fig. 30). Further study of these two ecologically very different forms in relation to the limits of the species would be very desirable.

The larger (up to about 70 mm long), solitary form has been collected at Speightstown, Six Men's Bay, Needham Point, Carlyle Bay, and Sandacres. It is very common on reefs, growing on the surface of and surrounded by the living coral tissue of a variety of species. The smaller (about 10 mm long) variety has been collected at Bathsheba, River Bay, and Oistins where it forms an encrustation on the limestone cliffs and platforms of the shore, at or below mean low tide level. It also occurs at Paynes Bay in fissures in the rock and at Six Men's Bay on the undersides of boulders left dry at low water. Similar colonies of this variety have also been seen at Conset Bay.

Spirobranchus giganteus is also present in the Jamaica collection, although only in the large, solitary form. It was taken at Lime Cay, Drunkenman's Cay, Ocho Rios, Montego Bay, and Morant Point.

This species appears to breed during the summer months. Ripe males and females of the smaller form have been found in May and June in Barbados. The larger form has been found to be mature in May and June in Barbados and in June and July in Jamaica. Studies on the smaller form show that it will spawn in the laboratory, by rupture of the body wall, and the embryos can be reared to the trochophore stage with no difficulty. The ova are coral pink in color and small in size, about 60 μ in diameter. At fertilization the germinal vesicle breaks down and a membrane is raised.

From cultures of fertilized eggs of this species, kept in bowls in the water table at normal surface water temperature (about 70° F), the following table of events during early development was obtained.

1 hour after fertilization	—first polar body
1½ hours	—second polar body
2 hours	—first cleavage, equal or almost
2½ hours	—second cleavage, equal
3 hours	—third and fourth cleavages, unequal
4 hours	—blastulae, 32 or more cells
5 hours	—beginning to swim
8 hours	—gastrulae
28 hours	—trochophores

The trochophores were fed on a culture of green, unicellular algae which developed spontaneously in a jar of standing sea water and some of the larvae were kept in this way as long as 15 days after fertilization. They fed well, swam actively until they were about 7 or 8 days old, and then tended to sink

to the bottom of the culture bowl where they moved slowly if at all. One small, transparent serpulid tube was formed in one of the culture bowls but the animal within died very soon and since no others were formed it is not known whether this single example was a metamorphosed *S. giganteus* or not.

The early trochophore (6 days old, Fig. 31) has a short posttrochal hemisphere, equivalent in size to the pretrochal region, a single red eyespot, an apical tuft, consisting usually of three long cilia and a prototroch underlaid by a band of pigment spots which appear red under reflected light and green under transmitted light. No telotroch could be seen at this stage. The digestive tract in these larvae consisted of three regions, a gullet opening from the mouth and lined with long, active cilia, an expanded stomach, separated from the gullet by a muscular sphincter and lined by small cilia, and a terminal, intestinal region opening to the outside by an anus located at the posterior tip of the animal. A few days later the posttrochal region had elongated (8 days old, Fig. 32); there is now a definite telotroch located anterior to the anus, a second eyespot has appeared, and the pigment spots beneath the prototroch have been lost. The oldest larvae kept alive and considered to be probably normal were 15 days old and had ceased to swim. Such a larva is illustrated in Fig. 33. The apical tuft appears to be reduced to a single, fairly thick cilium; the prototroch is divided into two rings with the mouth opening between the two. There is a short tuft of cilia at the anus which is now posterodorsal in position and another tuft at the posterior extremity of the animal, associated with a patch of clear red pigment. The upper part of the body, the pretrochal area, may now be seen to contract from side to side or to be flattened onto the prototroch by means of muscle fibers which traverse the cavity of the upper part of the body. The differentiation of the gullet and stomach regions is proceeding and the large, perhaps segmentally arranged cells of the posttrochal region are obvious, particularly on the ventral side of the body.

The adults of this species are always brilliantly colored on the thoracic membrane and branchial crown. Colors include blue, green, olive, red, pink, yellow, and white. Each individual animal bears a wide range of colors although the manner in which they are distributed over the body varies. Those parts of the body normally hidden in the tube are flesh-colored.

Salmacina incrustans Claparede, 1868

Salmacina incrustans Claparede, 1868, 436, Pl. 30, Fig. 5 (8); Fauvel, 1914, 328, Pl. 30, Figs. 26, 27 (12)

The specimens studied for identification came from the water table in the laboratory at the Bellairs Research Institute, Barbados. Several extensive colonies of this asexually reproducing serpulid established themselves in this way. The same species is common throughout the shallow water regions around Barbados, forming a delicate, white tracery on rocky surfaces. The toothed setae in the first thoracic segment separate this species from the closely related *S. dysteri*.

Discussion

Of the small sample of polychaetes reported here the majority (15) are known only from the eastern coast of tropical America. These are presumably stenothermal forms endemic to the region and their preponderance in the fauna is not unexpected, following a pattern established for other groups such as the crabs and echinoderms which have been studied more extensively.

Eight of the species discussed here are widely distributed polychaetes found in many parts of the world. Of these eight four are stenothermal, circumtropical forms and the rest are truly cosmopolitan, eurythermal species with ranges extending into the temperate regions.

Most studies of coastal invertebrates from tropical America have revealed a small number of species common to both Atlantic and Pacific coasts. In this study the proportion of such species is relatively high (six are reported) but this may be of little significance considering the small size of the total sample. Of the six three have been known before to have such a distribution and three, *Eunice tridentata*, *Pectinaria chilensis*, and *Phragmatopoma californica* were previously known only from the Pacific coast. Of the six all but one are apparently eurythermal with distributions extending into temperate waters. The exception is *E. tridentata* with a Pacific range from Lower California to Panama, indicating that this species may be limited to tropical and subtropical conditions.

Considering the small number of individuals concerned in this report the variety is considerable, as might be expected in a tropical community. This account is, however, too short and incomplete to permit further generalizations on the distribution or habits of West Indian Polychaeta and elaborations of this nature will have to wait until a greater body of information has been compiled.

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